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Sincerely,

On behalf of all authors

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## Special issue for Quaternary International journal

**TITLE SPECIAL ISSUE:** *"Peopling dynamics in the Mediterranean area between 45 and 39 ky ago: state of the art and new data".*

### **Macromammal and bird assemblages across the Late Middle to Upper Palaeolithic transition in Italy: an extended zooarchaeological review.**

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**Abstract**

Evidence of human activities during the Middle to Upper Palaeolithic transition is well represented from rock-shelters, caves and open-air sites across Italy. Over the past decade, both the revision of taphonomic processes affecting archaeological faunal assemblages and new zooarchaeological studies have allowed archaeologists to better understand subsistence strategies and cultural behaviors attributed to groups of Neandertal and modern humans living in the region.

This work presents the preliminary results of a 5-year research programme (ERC n. 724046 – SUCCESS) and offers a state-of-the-art synthesis of archaeological faunal assemblages including mammals and birds uncovered in Italy between 50 and 35 ky ago. The present data were recovered in primary Late Mousterian, Uluzzian, and Protoaurignacian stratigraphic contexts from Northern Italy (Grotta di Fumane, Riparo del Broion, Grotta Maggiore di San Bernardino, Grotta del Rio Secco, Riparo Bombrini), and Southern Italy (Grotta di Castelcivita, Grotta della Cala, Grotta del Cavallo, and Riparo l'Oscurusciuto). The available Number of Identified Specimens (NISP) is analysed through intra- and inter-site comparisons at a regional scale, while aoristic analysis is applied to the sequence documented at Grotta di Fumane. Results of qualitative comparisons suggest an increase in the number of hunted taxa since the end of the Middle Palaeolithic, and a marked change in ecological settings beginning with the Protoaurignacian, with a shift to lower temperatures and humidity. The distribution of carnivore remains and taphonomic analyses hint at a possible change in faunal exploitation and butchering processing between the Middle and Upper Palaeolithic. A preliminary comparison between bone frequencies and the distribution of burned bones poses interesting questions concerning the management of fire. Eventually, the combined use of relative taxonomic abundance

and aoristic analysis explicitly addresses time averaging and temporal uncertainty embedded in NISP counts and offers estimates of absolute change over time that can be used to support hypotheses emerging from taxon relative frequencies.

Keywords: Protoaurignacian, Uluzzian, Late Mousterian, Zooarchaeology, Aoristic analysis, Italy.

## 1 Introduction

Evidence for change in human behaviour and adaptive strategies linked to palaeoenvironmental change has been consistently documented for contexts dated to Marine Isotope Stage 3 (MIS 3: 60-30 ky BP) across Europe. The different subsistence strategies developed by Neandertals and modern humans in response to change in the underlying climatic conditions has been of particular interest in all transitional contexts of continental (references) and Mediterranean Europe (among others: Bietti and Manzi, 1990-91; Guidi and Piperno, 1992; Stiner, 1994; Bietti and Grimaldi, 1996; Milliken, 1999-2000; Kuhn and Bietti, 2000; Mussi, 2001; Peresani, 2011; Moroni et al., 2013).

Investigations into hominin diets, specifically those of the Neandertals, ineluctably feed into debates that revolve around the presumed capabilities, or lack thereof, of these hominins in the exploitation of small game as a food resource (Stiner, 2001; Stiner and Munro, 2002; Hockett and Haws, 2009).

Nevertheless, multiple data have induced some authors to suggest that the exploitation of small animals has been important for human subsistence since ca. 250ka (Klein and Scott, 1986; Stiner, 2005; Romandini et al., 2018b; Morin et al., 2019).

The Italian Peninsula plays a pivotal role as it connects Alpine Europe to the centre of the Mediterranean, and it provides a privileged perspective on interaction and replacement of

86 Neandertals by modern humans in a very diverse set of ecological and climatic regions  
87 (Benazzi et al., 2011; Higham et al., 2011; Peresani, 2011; Moroni et al., 2018; Villa et al.,  
88 2018, Peresani et al., 2019). All scholars agree for example on the role played by  
89 geographic barriers (Alps and Apennines) in segregating – from a climatic and ecological  
90 point of view – a western Mediterranean region from an eastern continental one, the latter  
91 affected by the cyclical emersion of the northern Adriatic platform (Sala, 1990; Sala and  
92 Marchetti, 2006). Such a diversity, however, made the reconstruction of past ecosystems,  
93 of the spatio-temporal distribution of resources, and of population-level subsistence  
94 strategies particularly difficult, especially in light of the intense glacial/interglacial cycles of  
95 the past 200,000 years. Notwithstanding the many detailed studies carried out at a local  
96 scale, a global understanding of change in mobility, adaptive strategies, and settlement  
97 pattern across the Middle-Upper Palaeolithic Transition across Italy is still elusive. The few  
98 exceptions (Van Andel and Davies, 2003) draw on very scant and heterogeneous data  
99 generated with different aims and at different scales, and the emerging scenarios are far  
100 from the temporal coherence exhibited by recent global (Bond et al., 1992; Dansgaard et  
101 al., 1993; Rasmussen et al., 2014) and Mediterranean palaeoclimatic and palaeological  
102 records (Allen et al., 1999; Sánchez Goñi et al., 2000; Tzedakis et al., 2002; Margari et al.,  
103 2009; Fletcher et al., 2010; Müller et al., 2011; Wulf et al., 2018).

104 The present paper aims to fill this gap and lay the foundations for a finer and more  
105 systematic comparison across the whole of the Italian Peninsula by presenting a state-of-  
106 the-art review of available data on faunal remains in a number of key Italian sites. By  
107 carefully documenting and comparing the distribution of faunal remains, we also generate  
108 hypotheses on the different subsistence strategies developed by Neandertals and modern  
109 humans in response to change in the underlying climatic conditions. Inferences about

paleoclimate and ecological settings are based on well-established links between ungulate families/avifaunal groups and the very specific environmental settings to which they were and still are adapted today. More specifically, the review focuses on relative taxon frequency of macromammals (ungulates, carnivores, rodents and lagomorphs) and birds across Late Mousterian, Uluzzian, and Protoaurignacian layers documented for 8 Italian sites for which quantitative data are available (Fig. 1, Areas 1-3). Other assemblages from central and northwestern Italy are also briefly described in this context, but their data are not directly integrated in more detailed investigations of regional trends. Finally, one particularly well-documented site (Grotta di Fumane) is also investigated through aoristic analysis, a probabilistic approach never before applied to the Palaeolithic of Italy. The method explicitly addresses temporal uncertainty and depositional factors affecting the observed number of specimens (NISP) and offers estimates of absolute change over time that can be used to support hypotheses emerging from taxon relative frequencies, as well as to allow a direct comparison between layers of different coeval sites. Finally, the available taphonomic evidence is also presented to provide preliminary insights on change over time in animal exploitation strategies and butchering processes.

This work is still preliminary, as it describes the initial results of an ongoing 5-year project aimed at reaching a deeper understanding of the mechanisms that underpinned the geographic overlap between Neandertals and modern humans in the Italian Peninsula, as well as the final replacement of the former by the latter. While future research will be able to support or disprove part of the picture that emerges from this first assessment, it nonetheless offers a first attempt to generate a coherent synthesis of all the data published to date concerning the region of interest.

## 2 Regional contexts

### 2.1 Northeastern (Adriatic) Italy

In the northern Adriatic Area archaeologists uncovered a considerable number of rock shelters and caves which yielded evidence of the last Neandertals and of the earliest modern humans. The geographic location of such sites is a key element to understanding regional differences in the faunal assemblages they have yielded (Sala, 1990; Sala and Marchetti, 2006; Sala and Masini, 2007; Masini and Sala, 2007, 2011). From a paleoecological point of view, pollen records from Lake Fimon and Azzano Decimo (northeastern Alpine foothills; Pini et al., 2009, 2010), document long-term vegetation trends during MIS 3. Phases of expansion of conifer-dominated forest (*Pinus sylvestris-mugo* and *Picea*), rich in broad-leaved trees (*Alnus* cf. *incana* and tree *Betula*), are accompanied by a reduction in the amount of warm-temperate elements (e.g. *Tilia*). Middle Würm stadials experienced summer temperatures very close to the growth limit of oaks, but still within the range of lime (MAW 13-15°C) which persisted, together with other temperate trees (e.g. *Abies*), up to ca. 40 ka (Pini et al., 2009, 2010; Badino et al., this Special Issue). Interestingly, peaks of *Tilia* pollen have been identified in layers preserving Mousterian artifacts and dated to 40.6-46.4 ka <sup>14</sup>C BP from cave deposits at the Broion shelter (Leonardi and Broglio, 1966; Cattani and Renault-Miskowski, 1984). Despite evidence of afforestation persisting at a long-term scale south of the Alps, forest withdrawals with expansion of grasslands and dry shrublands (Gramineae, *Artemisia*, Chenopodiaceae) occurred, possibly related to the establishment of drier/colder conditions (i.e. Greenland Stadials/Heinrich events). Such drier and colder stadal conditions likely favoured the presence of Alpine ibex, chamois, and marmot at low altitudes (in the Colli Berici), as well



157 as the presence of micromammals in steppic environments, and the diffusion of birds in  
158 tundra-like environments. The Po alluvial valley was, in contrast, inhabited by woolly  
159 rhinoceros, mammoth-, and bison (Sala, 1990).

160 Only a few contexts offer data on the Middle to Upper Palaeolithic transition, and their  
161 number further decreases for the temporal interval comprised between 50 and 35 ky.

162 At present, data on faunal remains and the relative chronology are available from Grotta di  
163 Fumane (Verona), Grotta Maggiore di San Bernardino (Vicenza), Riparo del Broion and  
164 Grotta del Broion (Vicenza), Grotta del Rio Secco (Pordenone) (Tab. 1, Fig. 1, Area 1).

165 **Grotta di Fumane** is a key site for northern Italy, located at 350 m asl in the western part  
166 of the Lessini Mountains (Tab. 1, Fig.1). Its archaeological sequence includes the Middle-  
167 Upper Palaeolithic transition (Peresani et al., 2008; Higham et al., 2009; López-García et  
168 al., 2015). Faunal assemblages consist of a rich association of ungulates, carnivores, and  
169 birds from diverse environments and climates. Quantitative comparisons between the  
170 Uluzzian assemblage (A3) (Tagliacozzo et al., 2013) and the late Mousterian ones (A4,  
171 A5-A6, A9) has highlighted only modest ecological and economic adjustments within a  
172 humid forested landscape (Peresani et al., 2011a,b; Romandini, 2012; Romandini et al.,  
173 2014a, 2016a,b, 2018a,b, Fiore et al., 2016; Gala et al., 2018; Terlato et al., 2019).

174 Considerable change, on the other hand, emerged from the Protoaurignacian occupations  
175 (A2), coinciding with a shift towards colder and steppic environments (Cassoli and  
176 Tagliacozzo, 1994a; Fiore et al., 2004).

177 **Riparo del Broion** is located in the northern part of the Berici eastern slope, at 135 m asl,  
178 along a steep slope comprising escarpments, cliffs and remnants of collapsed sinkholes  
179 that connects the top of Mount Brosimo (327 m asl) to the marshy and swampy plain (De  
180 Stefani et al., 2005; Gurioli et al., 2006; Romandini et al., 2012; Peresani et al., 2019).

181 FIGURE 1 HERE

182

183 Slope-waste clay deposits can be found at the feet of Mount Brosimo. Uluzzian faunal  
184 assemblages (levels 1f-1g) show a high richness due to the different environments of the  
185 surroundings. Alongside the presence of marmot, hare, chamois, ibex, bison and possibly  
186 aurochs, the number of red deer and roe deer bones as well as the abundance of wild  
187 boar remains indicate the existence of humid woodlands located in the alluvial plain to the  
188 east of Mount Brosimo (Peresani et al., 2019).

189 **Grotta Maggiore di San Bernardino** opens on the eastern slope of the Berici karst  
190 plateau 135 m asl, to the west of the alluvial plain of the Bacchiglione River. Eight  
191 lithological units compose a Middle-Late Pleistocene stratigraphic sequence (Cassoli and  
192 Tagliacozzo, 1994b; Peresani, 2001). The majority of the total faunal remains found at the  
193 site (78%) belongs to ungulates, although the frequency of ungulate remains varies  
194 between stratigraphic units (Tab. 1). Units II+III, associated to late Mousterian  
195 frequentation, is the only layer to have undergone a detailed zooarchaeological study. Its  
196 assemblage suggests the presence of humid climatic conditions, the expansion of  
197 woodlands (Cassoli and Tagliacozzo, 1994b; Peresani, 2011; López-García et al., 2017;  
198 Romandini et al., 2018b; Terlato et al., 2019).

199 **Grotta del Rio Secco** is located in a stream gorge at 580 m asl on the Pradis Plateau in  
200 the eastern part of the Carnic Pre-Alps (Fig. 1 and Tab. 1), an orographic system  
201 dissected by N-S and W-E valleys separating mountains with peaks of 2,000-2,300 m asl.  
202 The site is a flat and wide south-facing shelter, with a gallery completely filled with  
203 sediments. The outer area of the shelter presents with a heap of large boulders collapsed

from the original, larger roof. Human occupation has been dated (Tab. 1 and A.1) to the Late Mousterian (layers 5top, 7, 5, and 8) and to the Gravettian (layers 6 and 4) (Peresani et al., 2014; Talamo et al., 2014). In layers 7 and 8 archaeologists found evidence of the use of fire and of an intensive exploitation of carnivores (*Ursus arctos*, *Ursus spelaeus*, mustelids, and canids), which are more numerous than ungulates (Peresani et al., 2014; Romandini et al., 2018a). Although bird remains are rare, a terminal pedal phalanx of a golden eagle with anthropic cut marks on the proximal articular facet was recovered from layer 7 (Romandini et al., 2014b).

## 2.2 Northwestern Italy (Tyrrhenian) Italy

The coastal area of this region is characterized by a particular relief pattern with middle-range mountains and a narrow littoral plain between the Mediterranean Sea and the southern Alps (Fig. 1). Faunal assemblages of the region date to between Marine Isotope Stage (MIS) 6 and 3, in agreement with geochronological, pollen and cultural data (Valensi and Psathi, 2004; Bertola et al., 2013; Romandini, 2017). From a general point of view, faunal assemblages attributed to the Middle to Upper Palaeolithic transition exhibit high taxonomical richness, reflecting a variety of biotopes such as forest hills, coastal plains, narrow valleys in the hinterland and numerous cliffs. Consistently high values in species richness, in particular for carnivores, were recorded in Liguria during MIS 3 and 2 (Valensi and Psathi, 2004). The most frequent species of ungulates and small mammals point to the extensive presence of forested environments.

A variety Late Mousterian sites are reported (Fig. 1): Arma delle Manie, Caverna delle Fate, Grotta degli Zerbi, Santa Lucia Superiore, Via San Francesco, Riparo Bombrini, Riparo Mochi, Grotta del Principe in Italy, and Grotte de l'Observatoire in the Principality of

228 Monaco. The arrival of modern humans in the region is associated to a marked change in  
 229 the archaeological record (Negrino and Riel-Salvatore, 2018; Riel-Salvatore and Negrino  
 230 2018a). At present, Protoaurignacian evidence has been uncovered at Riparo Mochi  
 231 (Alhaique, 2000; Kuhn and Stiner, 1998; Douka et al., 2012; Grimaldi et al., 2014), Riparo  
 232 Bombrini (Bertola et al., 2013; Holt et al., 2019; Negrino and Riel-Salvatore 2018; Riel-  
 233 Salvatore et al. 2013; Riel-Salvatore and Negrino 2018a, 2018b; Vicino 1984), Arma degli  
 234 Zerbi and Grotte de l'Observatoire (Rossoni et al., 2016; Onoradini, 2004; Onoradini and  
 235 Simon, 2006; Porraz et al., 2010; Romandini 2017).

### 236 **2.3 Southern Italy**

237

238 Palaeoecological data for southern Italy come from the Lago Grande di Monticchio record  
 239 (Monte Vulture, Basilicata). During MIS 3, pollen data associations indicate an alternation  
 240 between cold/dry steppic vegetation (*Artemisia*-dominated steppe/ wooded steppe),  
 241 related to Greenland Stadials/Heinrich events (GSs/HEs), and an increased range of  
 242 woody taxa including deciduous *Quercus*, *Abies* and *Fagus* (up to 30–60% of arboreal  
 243 pollen), referred to Greenland Interstadials (GIs) with a maximum expansion between ca.  
 244 55-50 ka (i.e. GI 14) (Allen et al., 1999; Fletcher et al., 2010; Badino et al., this Special  
 245 Issue). Nevertheless, faunal assemblages coming from MIS3-aged stratigraphic  
 246 sequences highlight different climatic trends between Tyrrhenian (southwestern) and  
 247 Ionian (southeastern) contexts (Boscato 2017) due to an almost persistent moisture  
 248 availability on the former, mainly generated by the orographic uplift of air charged with  
 249 moisture from the Tyrrhenian Sea, and to Balkan influence on the latter. The Ionian area is  
 250 characterized by open environment taxa (e.g. *Bos primigenius*) while the Tyrrhenian one  
 251 shows an abundance of forest species (Cervidae).

252

## 253 2.3.1 Central-southwestern (Tyrrhenian) Italy

254 Southwestern Italy (Tyrrhenian Area – Area 2, Fig. 1) is best represented by **Grotta di**  
 255 **Castelcivita** (Salerno). This site is located 94 m asl and is about 20 km far from the  
 256 modern coastline, in a territory encompassing the valley of the Calore river and the Alburni  
 257 mountains (m 1742). The archaeological sequence is dated to MIS 3 (Gambassini, 1997)  
 258 and is about 2.5 m thick. The lowermost portion (layers cgr, gar, lower rsi, spits 32-  
 259 18lower) contains Late Mousterian deposits and is overlaid by Uluzzian layers (upper rsi,  
 260 pie, rpi, rsa'', spits 18upper-10lower). The sequence is capped by Protoaurignacian layers  
 261 (rsa'-gic-ars, spits 10upper-top of sequence), which are sealed by the Campanian  
 262 Ignimbrite (Giaccio et al., 2017). From a zooarchaeological point of view, a unique aspect  
 263 of this site is the presence of freshwater fish in all chronological phases (Cassoli and  
 264 Tagliacozzo, 1997).

265 **Grotta della Cala** (Marina di Camerota – Salerno) opens close to the present coastline  
 266 into a steep calcareous cliff which is part of a hilly/mountain range characterized by  
 267 plateaus and valleys. The MIS 3 coastline was about 5 km from the cave entrance. The  
 268 stratigraphic sequence is about 3 m thick and starts from the bottom with Middle  
 269 Palaeolithic layers in a succession of stalagmites and clastic sediments (Martini et al.,  
 270 2018). At the entrance of the cave, the Middle Palaeolithic is followed by early Upper  
 271 Palaeolithic deposits, containing Uluzzian (spit 14) and Protoaurignacian (spits 13-10)  
 272 evidence (Benini et al., 1997; Boscato et al., 1997). These are covered, after a  
 273 stratigraphic hiatus, by Gravettian, Epigravettian, Mesolithic and Neo-Eneolithic layers  
 274 (Palma di Cesnola, 1993).

275 Beyond these well-documented sites, the only other Uluzzian deposit with faunal  
 276 assemblages in the region is documented at the Tuscan site of Grotta la Fabbrica  
 277 (Grosseto; Pitti et al., 1976). Here the abundance of equids points to open environments  
 278 (less evident in the Protoaurignacian layers). As far as the Late Mousterian is concerned, a  
 279 similar faunal composition is recorded at Buca della Iena (Lucca; Stiner 1994). Cervidae  
 280 are, in contrast, the most abundant family in coeval deposits of Grotta dei Santi (Monte  
 281 Argentario, Grosseto), suggesting a more humid/temperate climate. In Latium a  
 282 temperate/humid phase connoted by abundant auroch and deer remains is recorded at  
 283 Grotta del Fossellone (Alhaique and Tagliacozzo, 2000) and at Grotta di S. Agostino  
 284 (Stiner, 1994). A similar trend is found at Grotta Breuil (Alhaique and Tagliacozzo, 2000)  
 285 where Cervidae are the most abundant in layers 6 and 3a, although ibex remains become  
 286 more frequent in the latter. In Campania, at Riparo del Poggio (Marina di Camerota),  
 287 located near Grotta della Cala, faunal assemblages are dominated by Cervidae and are  
 288 typically linked to temperate climates (fallow deer is the most abundant species; Boscato  
 289 et al. 2009).

290

### 291 2.3.2 Central - southeastern (Adriatic-Ionian) Italy

292 In the Ionian area (Fig. 1) **Grotta del Cavallo** opens into the rocky coast of Uluzzo Tower  
 293 Bay, at the margin of a vast rolling plain. This cave contains a 7- meter thick stratigraphy  
 294 which has at its bottom a marine conglomerate attributed to MIS 5e. This is overlaid by a  
 295 Mousterian sequence dated between MIS 5 and MIS 3 (Tab. A.1) (layers N-FI). These  
 296 layers are followed by an Uluzzian sequence (EIII – DIb; Moroni et al., 2018) sandwiched  
 297 between two *tephra* layers (Fa and CII) attributed to the Y-6 and the Y-5 (Campanian  
 298 Ignimbrite) events, respectively (Zanchetta et al., 2018).

299 **Riparo l'Oscurusciuto** opens inside the ravine of Ginosa (Taranto), to the north of the  
300 modern village and about 20 km from the present coastline (Fig. 1). The zooarchaeological  
301 data suggest that Neandertal hunters exploited both the main regional environments, i.e.  
302 forest steppe located on flat hills and forested area on the humid bottom of the gorge.  
303 The Middle Palaeolithic stratigraphy is 6-meter thick. A tephra (US 14) attributed to the  
304 Green Tuff of Monte Epomeo (Ischia) and dated to ca. 55 ky seals the surface of a living  
305 floor currently under excavation (US 15) (Boscato et al., 2004; 2011; Boscato and  
306 Crezzini, 2006, 2012; Boscato and Ronchitelli, 2008). All the cultural assemblages  
307 investigated can be referred to MIS 3 and fall in a chronological interval of ca. 12,000  
308 years. Recurrent Levallois is the most abundant lithic production system (Marciani et al.,  
309 2016, 2018, Spagnolo et al., 2016, 2018;).  
310 In Molise (Adriatic area) Grotta Reali (Rocchetta a Volturno) yielded Late Mousterian  
311 assemblages mostly consisting of Cervidae that can be linked to cold and humid climatic  
312 conditions (Sala et al., 2012).

313

### 314 **3 Materials and Methods**

315 Of all the archaeological contexts mentioned in the introduction, the present research only  
316 focuses on the 8 ones that present with quantitative evidence on the distribution of faunal  
317 assemblages in Middle-to-Upper Palaeolithic transition deposits across Italy (> 50-35 ky,  
318 Tab. 1, A.1 and Fig. 1). Sampled archaeological sites were grouped into three geographic  
319 areas based on site location and ecological/environmental context: 1) Northeastern Italy (4  
320 sites); 2) Southwestern/Tyrrhenian Italy (2 sites) and 3) Southeastern/Ionian Italy (2 sites;  
321 Fig. 1). New zooarchaeological data for Northwestern Italy are now available from Riparo  
322 Bombrini (Pothier Bouchard et al., this issue), while for the southeastern/Ionian area the

323 zooarchaeological analysis from Grotta di Uluzzo C is currently in progress (Fig. 1). Both  
324 sites are part of the ERC n. 724046 – SUCCESS project, but they are not included in the  
325 present synthesis.

326 All faunal remains used to compute species abundance based on taxon frequency were  
327 uncovered by sieving sediment using 0.5mm and 1mm meshes in Northeastern,  
328 Southwestern, and Southeastern Italy. Based on currently available evidence, specimens  
329 were nonetheless grouped into three size classes in Northeastern Italian contexts (0.1-  
330 1cm, 1-3cm, >3cm; Tab. 2) and into two size classes in Southwestern and Southeastern  
331 Italian contexts (1-3cm, >3cm; Tab. 5).

332 Different sources of surface bone alteration (anthropic cut marks vs. animal tooth marks,  
333 trampling, postdepositional and modern modifications generated during excavation) were  
334 discriminated drawing criteria outlined in a on well-established body of taphonomic  
335 literature (Binford, 1981; Potts and Shipman, 1981; Shipman and Rose, 1984;  
336 Blumenshine and Selvaggio, 1988; Capaldo and Blumenshine, 1994; Lyman, 1994;  
337 Blumenshine, 1995; Fisher, 1995; Fernández-Jalvo and Andrews, 2016; Duches et al.,  
338 2016). The degree of combustion was estimated using the method developed by Stiner et  
339 al. (1995) and, in Northeastern Italian contexts, burned and calcined bones were  
340 separated from unburned materials.

341 Faunal remains were attributed to species and genus and, when these were not  
342 determinable, to families. Unidentified mammal bones were grouped into three classes  
343 based on body size: large (red deer, moose, giant deer, bison, aurochs, horse, lion and  
344 bear); medium (alpine ibex, chamois, roe deer, fallow deer, wild boar, wolf, lynx, leopard  
345 and hyena); and small (hare, marmot, beaver, mustelids, wild cat and fox). In addition,  
346 unidentified specimens from the southern sites were grouped according to anatomical



categories such as “skull”, “jaw”, “teeth”, “vertebrae”, “ribs” etc. or more general categories such as “epiphysis” “diaphysis” and “spongy bones”.

As far as northern Italy is concerned, taxonomic and skeletal identification were based on the reference collections stored at the Bioarchaeology Section of the National Prehistoric Ethnographic Museum “Luigi Pigorini” (Lazio Museum Pole, Rome), at the Prehistoric and Anthropological Sciences Section in the Department of Humanities, University of Ferrara and at the Laboratory of Osteoarchaeology and Palaeoanthropology at the Department of Cultural Heritage, University of Bologna (Ravenna). Bone assemblages recovered from the southern Italian sites were compared with the reference collection stored at the Research Unit of Anthropology and Prehistory of the University of Siena. Differences between the Uluzzian layer of Grotta del Cavallo and the Late Mousterian layers at Grotta del Cavallo and Riparo l'Oscurusciuto (i.e. the only layers which displayed no sign of carnivore activity on ungulate bones) were formally assessed for percentages of carpal and tarsal bones, and of phalanges and sesamoides (relative frequencies were based on both total ungulate counts and on the remains of *Bos Primigenius*). In addition, the presence of significant differences was tested for remnant diaphysis, epiphysis, and spongy bones between the same layers. To do so we measured effect size as Cohen's  $h$  using the function ES.h in the package pwr in R (Champely, 2018), we then measured statistical power using the dedicated pwr.2p2n.test function in the same package, and performed a two-tailed test for equality in proportions between the chosen layers (with continuity correction for cases in which the number of successes or failures was lower or equal to 5; Tab. A.13 – A.17). We also tested the hypothesis of differences in the degree of fragmentation across sites of Northern Italy by running arcsine transformation of proportions fragment-size classes at all sites (1-3cm, >3cm; following Morin et al. 2019)

371 and then comparing the distribution of transformed values between Uluzzian and Late  
372 Mousterian layers via a two-tailed Mann-Whitney test for independent sample design. As  
373 for southern Italy, we once again only focused on Riparo l'Oscurusciuto and Grotta del  
374 Cavallo in Southeastern Italy. We tested for significant differences in proportions and also  
375 calculated effect size and statistical power to support the obtained results.

376 Species abundance was quantified using the Number of Identified Specimens (NISP;  
377 Grayson, 1984). Notwithstanding its limitations (e.g. inflation of the count of rare parts,  
378 lower predictive power when limited to long bones), this particular species estimate offers  
379 accuracy and reproducibility at the ratio scale (Morin et al., 2017). The ubiquitous  
380 recording of NISP in all the examined contexts made it the best available method to  
381 directly compare different sites across the study region. Once NISP of each mammal and  
382 avian group or species was obtained for all layers of the 8 sampled archaeological sites  
383 across Italy, we grouped layers belonging to the same region (i.e. Northeastern,  
384 Southwestern, and Southeastern Italy) and within each region we ordered them into a  
385 single diachronic sequence, based on absolute dates (Tab. 1 and A9) and associated  
386 material cultural evidence. Relative taxon abundance was calculated in each layer and  
387 variability in relative frequency over time was inspected through bar charts, in order to  
388 highlight any differences between trends emerging in different regions.

389 Comparing NISP proportions across different archaeological layers (in the same context or  
390 between different contexts), however, presents a number of potential issues. In addition to  
391 post-depositional processes, substantial differences in the time of accumulation of different  
392 layers may have deleterious effects on the accurate representation of faunal spectra. This  
393 process, known as time-averaging, is extremely frequent in geologic and anthropic  
394 contexts (Binford, 1981; Kowalewski 1996; Premo, 2014; Madsen, 2018), and has a direct

395 impact on the reliability of the quantification of abundance, richness, evenness, and  
396 diversity in time-averaged samples (Leonard and Jones, 1989). Specifically, the longer the  
397 duration of layer formation, the more inflated richness and diversity will be. This makes  
398 tracking change over time more problematic and increases the risk of misidentifying  
399 inflated counts for actual human choices (i.e. Type I error when testing hypotheses;  
400 Premo, 2014; Madsen, 2018). The presence of differential accumulation rates,  
401 palimpsests, and taphonomic processes therefore complicates any attempt at quantifying  
402 the effective temporal scale of individual layers solely based on stratigraphy.

403 In addition, inference made by comparing NISP proportions is hampered by the limitations  
404 of closed datasets (Lyman, 2008; Orton et al., 2017). Species relative frequencies are by  
405 definition computed over the total number of collected remains and their sum is bound to  
406 be equal to 1. No relative frequency is free to vary over time without affecting or being  
407 affected by change in the frequency of another class, i.e. the relative abundance of one  
408 particular taxon will always be negatively correlated to the relative abundance of another  
409 taxon. Interpreting such increases and decreases as the effect of some independent  
410 mechanism (e.g. environmental change, cultural selection) is therefore not always  
411 straightforward.

412 In order to overcome the limitations mentioned above while providing support for the  
413 trends that might emerge from relative taxonomic abundance analysis across the time-  
414 ordered layers of different sites, we also built long-term time-series of zooarchaeological  
415 data documented at Grotta di Fumane (Northeastern Italy) that can directly be compared  
416 against independent sources of information (e.g. palaeoclimatic models, palinological and  
417 palaeoenvironmental data), and across mismatched and differentially overlapping

418 contexts. Grotta di Fumane was chosen as a case study because it offers the longest and  
419 best-dated sequence among all the available sites.

420 More specifically, we computed aoristic sums (i.e. the sum of the probability of existence of  
421 all events for a given temporal interval) of taxon abundance to obtain estimates of taxon  
422 frequency based on absolute radiocarbon dates. Aoristic analysis has been already  
423 employed in a few archaeological and zooarchaeological studies (Ratcliffe, 2000; Johnson,  
424 2004; Crema, 2012; Bevan et al., 2013; Orton et al., 2017), although the method is still  
425 generally rarely used and, to the best of our knowledge, it has never been applied to  
426 palaeolithic contexts. This approach consists of: a) assigning a start and end date to each  
427 archaeological layer from which fossil fragments had been retrieved; b) dividing the entire  
428 time span of the study period into temporal bins of fixed width; c) based on the start and  
429 end dates of the relevant layer, and drawing on Laplace's principle of insufficient reason  
430 (see Crema, 2012; Orton et al., 2017 for a detailed discussion), dividing the total  
431 probability mass of each deposition event/fragment (equal to 1) across the  $t$  temporal bins  
432 comprised in the date interval of the layer. Each deposition event therefore exhibits a  
433 uniform probability of existence at each bin calculated as  $1/t$ ; d) summing all the  
434 probabilities falling in the same bin, and repeating the same operation for the entire study  
435 period.

436 The result is an estimate of species frequency distribution which incorporates all the  
437 temporal uncertainty embedded in the data. Better dating leads to shorter temporal  
438 intervals for each deposition event, that in turn allows researchers to assign a higher  
439 probability of existence at each temporal bin. As a consequence, worse dating leads to  
440 higher dispersion in the probability of existence, i.e. to stable time series which do not  
441 show clear evidence of increase or decrease as an artefact due to lack of resolution. In the

present work, we first set the temporal limits for each layer at Grotta di Fumane. When start and end dates were already available from the literature (as in the case of layers A9) these intervals were directly taken (Tab. A. 9). As far as all the remaining layers are concerned (A6, A5/A5+A6, A4, A3, and A2), the most recent available C14 dates (Higham 2011; Douka et al. 2014) were calibrated using the IntCal13 curve (Reimer et al. 2013; Ramsey and Lee, 2013) in OxCal 4.3 (Bronk Ramsey 2009), and start/end dates were estimated as the median of the posterior probability distribution of layer boundaries generated by grouping calibrated dates into overlapping/sequential phases using the same software (Fig. A.1-A.2). This particular model was chosen to fully exploit the potential of aoristic analysis and considering that at this site Uluzzian and final Mousterian are reported as temporally indistinguishable (Douka et al. 2014; Peresani et al., 2016; Falcucci et al., 2017).

Raw NISP counts were then used to compute aoristic sums of each taxon across 50-year bins through the function *aorist* in the package *archSeries* in R version 3.4.4 (Orton, 2017, R Core Team 2018). To avoid generating artifacts due to empty bins at the interval 41600-41100 cal BP, 10 years were added to the median date for the end boundary of level A3. Taxon-specific aoristic values were then summed and used to calculate estimates of taxon relative frequencies. To further ascertain the presence of absolute shifts in estimated frequency, we also plotted the aoristic sum of ungulates. In this case, absolute frequency estimates were compared against 95%-confidence envelopes generated through Monte-Carlo simulation (n. iterations=5000) as well as against a dummy model generated assuming a uniform frequency distribution following Crema (2012) and Orton (Orton et al., 2017). Both the empirical and dummy simulations were computed using the function *date.simulate* in the package *archSeries*. Using the same function, rates of change were

also computed for ungulate families. The aim was to assess whether there were temporal bins exhibiting shifts in the abundance of families compared to other bins. Following Crema (2012) and Orton (2017), rates of change were examined by observing (in this case through boxplots) the distribution of simulated standardised differences between each chronological bin and the preceding one. Temporal intervals with median and interquartile range falling above the zero line (suggesting stability or absence of change) were interpreted as a sign of increase, while boxes falling under the zero line were interpreted as instances of decrease. Such distributions were compared against the 95% confidence envelopes of the null model based on the aoristic sum of carnivores, which provides a null expectation independent from palaeoenvironmental change.

#### 4 Results

Northeastern Italian contexts yielded a total of 323,964 remains (NISP=9,044) while for Southern Italy as a whole 33,340 remains were documented (NISP=2,351). From a zooarchaeological point of view, Late Mousterian layers have been investigated more intensively than later ones in both regions. Despite the difference in absolute counts, the proportion of mammal orders and classes is roughly the same across all contexts (Fig. 2), with ungulates being the most abundant category followed by carnivores, birds (at Grotta di Fumane and Castelcivita), and rodents, in decreasing order of importance.

Uluzzian layers exhibit an increase in the relative abundance of carnivore and bird remains, matched by a considerably lower number of remains attributed to large rodents (e.g. marmot and beaver) and lagomorphs (Fig. 2). Protoaurignacian phases invert this trend, with an appreciable decrease in the number of carnivore and bird remains.

FIGURE 2 HERE

490

491 **4.1 Mammals**

492 Despite the specificities that may bias the abundance of faunal remains in each of the  
493 examined contexts (e.g., Grotta del Rio Secco being consistently used by bears which, in  
494 turn, were routinely exploited by Neandertals; Romandini et al., 2018b), Late Mousterian  
495 contexts in Northeastern Italy show an increase in the prevalence of cervidae, followed by  
496 a decrease of *Cervus elaphus* and *Capreolus capreolus* matched by a gradual increase, in  
497 the Uluzzian and Protoaurignacian, in caprinae – especially *Capra ibex* and *Rupicapra*  
498 *rupicapra* (Fig. 3 and Tab. A.1). This change over time in the relative abundance between  
499 cervidae and caprinae may hint at a shift from a temperate climate characterised by  
500 forests and meadows to an alpine setting with open environments.

501 The archaeological sites are located in a region that included habitats suitable for bovineae,  
502 ranging from dense forests with wetlands and small streams more attractive to *Bos*  
503 *primigenius*, to hilly grasslands and plains, populated by bison. However, bovids are  
504 generally less abundant than the previous families, and their presence remains roughly  
505 constant across the entire study sequence.

506 Moose (*Alces alces*) and giant deer (*Megaloceros giganteus*) are less frequent and well  
507 attested in Mousterian and Uluzzian layers. Their presence suggests – during this period –  
508 the existence of humid woodlands near the sampled archaeological sites. Wild boar is  
509 rarer yet, being present anecdotally in the Late Mousterian at Grotta di Fumane, while it is  
510 more abundant at lower elevations (Grotta di San Bernardino, Mousterian Units II + III;  
511 Riparo del Broion, Uluzzian layers 1e+1f+1g). The presence of woolly rhinoceros  
512 (*Coelodonta antiquitatis*) in the Uluzzian layer A3 at Grotta di Fumane and of

*Stephanorhinus* sp. at Grotta di San Bernardino indicates decreasing temperatures and presence of cold arid conditions.

FIGURE 3 HERE

In this region, carnivores are more represented in Late Mousterian and Uluzzian assemblages, while their frequency steadily decreases in Protoaurignacian layers (Fig. 2). Nevertheless, carnivores increase beginning with the Uluzzian (Romandini et al., 2018a), and the presence of wolverine (*Gulo gulo*), ermine (*Mustela erminea*), and arctic fox (*Alopex* cfr. *lagopus*) further supports the onset of colder and arid climate conditions during the MP-UP transition (Fig. 4, Tab. A.2). Rodents and lagomorphs (Tab. A.3) are represented by beaver and marmot, already present in Late Mousterian assemblages, and by lagomorphs in the Uluzzian and Protoaurignacian (Romandini et al., 2018a). Upper Palaeolithic contexts also yielded remains of *Lepus* cfr. *timidus*, further supporting the diffusion of increasingly colder environments in the latest phase of the studied sequences.

FIGURE 4 HERE

In Southwestern/Tyrrhenian Italy, the Late Mousterian sequence at Grotta di Castelcivita (spits 32-24) yielded a conspicuous amount of cervidae fragments (*Cervus elaphus*, *Dama*, *Capreolus capreolus*); fallow deer in particular is the most abundant species (Fig. 5 and Tab. A.4). Later on, in spits 23-18 lower, there is an increase in the abundance of red and roe deer and of chamois (*Rupicapra* sp.), correlated to an increase in humidity (Masini and Abbazzi, 1997). The beginning of the Uluzzian sequence (spits 18 upper-15) is



characterised by higher frequencies of horse (*Equus ferus*) and large bovids (*Bison priscus* and *Bos/Bison*) suggesting the occurrence of colder climates and sparse woodland. In the following Uluzzian layers (spits 14-10 lower), an additional increase in the occurrence of equids and a decrease in the frequency of fallow deer suggest more open environments. The Early Protoaurignacian (spits 10 upper – 8 lower) shows comparable environmental conditions, while spits 8 upper-7 can be linked to an increase in woodland cover as suggested by the higher presence of deer and the decrease in the frequency of horse (Fig. 5 and Tab. A.4), followed by cold-temperate phases (spit 6) (Masini and Abbazzi, 1997). The anthracological evidence supports the climatic and ecological trend inferred from zooarchaeological remains (Castelletti and Maspero, 1997).

FIGURE 5 HERE

At Grotta della Cala (Marina di Camerota, Salerno), faunal remains from the Uluzzian (spit 14) are characterised by a conspicuous presence of cervidae (representing on the whole 74% of ungulates) and in particular of fallow deer, typical of temperate climates and Mediterranean evergreen forest. In the Protoaurignacian layers (spits 13-10), lower frequencies of fallow deer and higher frequencies of red deer indicate the onset of colder conditions (Fig. 5 and Tab. A.4). Low frequencies of ungulates linked to open environments/wooded steppe (such as horse, alpine ibex and aurochs) are also recorded (Benini et al., 1997). Cervids account for over 70% of the ungulates recovered in these layers (Boscato et al., 1997).

In the same region, carnivores occur in all phases. Whilst in the Middle Palaeolithic, most of the remains are referable to the spotted hyaena and the leopard, species richness

increase in the Uluzzian and in the Protoaurignacian (Tab. A.5). Rodents and lagomorphs are very rare.

The record of Southeastern/Ionian Italy, on the other hand, is based on the sequences uncovered at Riparo l'Oscurusciuto (Ginosa – Taranto) and Grotta del Cavallo (Nardò – Lecce) (Fig. 1, 6 and Tab. A.6). At Riparo l'Oscurusciuto, layers 15:4 are characterised by the substantial presence of *Bos primigenius*, counterbalanced by low frequencies of horse, rhinoceros and caprinae, and by anecdotal frequencies of cervidae (especially fallow deer), all of which hints at an environment characterised by wooded meadows and open spaces (Fig. 6). Aurochs is less frequent in SU 3, while in the same unit, deer is more abundant, the presence of rhinoceros can be inferred by tooth fragments, and horse becomes the most represented ungulate (Tab. A.6). At the end of the sequence (SU2-1), aurochs is once again the most abundant ungulate, while the increase in abundance of fallow deer suggests the onset of a temperate phase (Boscato and Crezzini, 2012).

FIGURE 6 HERE

The Late Mousterian sequence at Grotta del Cavallo (layers FIII-FI) also yields evidence of the climatic fluctuations known for MIS 3 (Tab. A.1), which agrees with the sequence described for Riparo l'Oscurusciuto. An initial phase characterised by open/steppic forests indicated by the dominance of aurochs remains (layer FIIIE) is followed, in layers FIIID-FIIIB, by a more temperate phase (as suggested by higher frequency of fallow deer) and by a third, more arid stage in layers FIII-FI associated with the presence of aurochs and horse (Sarti et al., 2000; 2002) (Tab. A.6). The lowermost Uluzzian level EIII5 suggests, in contrast, a shift to an increasingly colder climate with more dispersed woodlands, indicated

by the absence of fallow deer and by the increased presence of horses (Tab. A.6; Boscato and Crezzini, 2012).

With the only exception of red fox which has been found in the Late Mousterian of Grotta del Cavallo, carnivores, rodents and lagomorphs are almost absent in the assemblages of Ionic area (Tab. A.7).

## 4.2 Avifaunal remains

Substantial evidence on the exploitation of avifauna was documented for Grotta di Fumane and Grotta di Castelvita (Cassoli and Tagliacozzo, 1994b, 1997; Masini and Abbazzi, 1997; Gala and Tagliacozzo, 2005; Peresani et al., 2011a; Romandini, 2012; Tagliacozzo et al., 2013; Fiore et al., 2016; Romandini et al., 2016a, b; Gala et al., 2018; Fiore et al., in this issue).

The bird species identified at Grotta di Fumane belong to the extant Italian avifauna (Tab. A.8) with the exception of the willow grouse (*L. cf. lagopus*), a boreal species which has historically never been observed in Italy. The parrot crossbill (*L. pytyopsittacus*) is another boreal species currently found in Northern Europe and considered a vagrant species in Italy (Brichetti and Fracasso, 2015). Taxa linked to open and rocky environments are the most abundant (Fig. 7). More specifically, bearded vulture (*G. barbatus*), golden eagle (*A. chrysaetos*), red-billed and yellow-billed chough (*P. pyrrhocorax* and *P. graculus*), common raven (*C. corax*), Eurasian crag martin (*P. rupestris*) and white-winged snowfinch (*M. nivalis*) indicate the presence of rocky cliffs, while treeless terrain with rocky outcrops is indicated by rock partridge (*A. graeca*) and rock ptarmigan (*L. muta*). On the other hand,

609 the presence of wooded areas in the surroundings of the cave is indicated by the black  
 610 grouse (*L. tetrix*), stock dove (*C. oenas*), common woodpigeon (*C. palumbus*), Boreal owl  
 611 (*A. funereus*), tawny owl (*S. aluco*), white-backed woodpecker (*D. leucotos*, currently  
 612 reduced to small populations in the Central Apennines but once more widespread; Pavia,  
 613 1999, Brichetti and Fracasso, 2007) Eurasian jay (*G. glandarius*), and Eurasian bullfinch  
 614 (*P. pyrrhula*). The presence of the northern nutcracker (*N. caryocatactes*) and parrot  
 615 crossbill (*L. pytyopsittacus*) also point to the presence of coniferous forests. Additionally,  
 616 open grasslands and wet meadows are indicated by common quail (*C. coturnix*), grey  
 617 partridge (*P. perdix*), corncrake (*C. crex*, which was breeding in the surroundings of the  
 618 cave, as attested by the finding of juvenile bones) and northern lapwing (*V. vanellus*),  
 619 while willow grouse (*L. cf. lagopus*) is an indicative of tundra-like open areas such as  
 620 moors and peatlands. Finally, the presence of two duck species (*A. platyrhynchos* and *A.*  
 621 *cf. crecca*) and two Rallidae (*R. aquaticus* and *cf. G. chloropus*) suggests nearby wetlands  
 622 or slow-flowing water courses (Cramp, 1998).

623 As a whole the bird assemblage at Fumane points to an Alpine ecological setting with  
 624 forests and open areas. Several identified bird species (rock ptarmigan, black grouse,  
 625 Boreal owl, bearded vulture, white-backed woodpecker, red and yellow-billed chough,  
 626 Northern nutcracker and white-winged snowfinch) currently live in Italy at considerably  
 627 higher altitudes than Fumane. The presence of their fossils remains at 350 m asl suggests  
 628 the downward shifting of the vegetational zones during MIS 3 due to a decrease in climate  
 629 value parameters. The presence of remains probably belonging to willow grouse in layer  
 630 A6 and to parrot crossbill in layers A1+A2 during two of the harsher climatic phases  
 631 (Heinrich Event 5 and Heinrich Event 4 respectively) (López-García et al., 2015) might be

632 an example of two boreal species seeking a *refugium* in Mediterranean Europe (Tyrberg,  
633 1991; Carrera et al., 2018a,b).

634 The relative frequency of species related to forest, open, rocky and water environments  
635 calculated for each layer (Fig. 7) suggests the presence of temperate conditions for layer  
636 A9, followed by a colder climate in A6. The species linked to open environments decline  
637 sharply in layer A4 (attributed to the GI12 interstadial) before increasing anew in layer A3,  
638 marking the beginning of Heinrich Event 4 that lasts until the end of the sequence (López-  
639 García et al., 2015). Heinrich Event 4, however, did not prevent the persistence of open  
640 forests, as attested by the bird taxa found in A1+A2 and A3. The apparent increase of  
641 forest bird taxa in the layers corresponding to Heinrich Event 4 could be explained by a  
642 switch from anthropic to natural accumulation in the Protoaurignacian, as suggested by the  
643 lack of anthropic marks on bird bones.

644 FIGURE 7 HERE

645 Turning to Grotta di Castelcivita, while the bird remains have been the object of a recent  
646 taphonomic revision (Fiore et al. in this issue), the data discussed here are drawn from  
647 Cassoli and Tagliacozzo (1997). All identified taxa belong to the extant Italian avifauna  
648 (Tab. A.8 and Fig. 8, Cassoli and Tagliacozzo, 1997; Brichetti and Fracasso, 2015; Gala et  
649 al., 2018). In terms of NISP, the vast majority are from open and rocky environments. The  
650 presence of extensive wetlands and marshes near the cave is suggested by several duck,  
651 wader and gull species (*A. nyroca*, *S. querquedula*, *M. strepera*, *M. penelope*, *A.*  
652 *platyrhynchos*, *A. crecca*, *P. squatarola*, *N. phaeopus*, *L. limosa*, *A. interpres*, *C. pugnax*,  
653 *G. media*, *L. ridibundus*). The red-billed chough (*P. pyrrhocorax*), yellow-billed chough (*P.*  
654 *graculus*) and Eurasian crag martin (*P. rupestris*) are indicative of rocky cliffs, while rock  
655 partridge (*A. graeca*) attests to the presence of treeless rocky terrain. Open areas such as

656 grasslands, steppe and shrublands were also present, as indicated by the common quail  
657 (*C. coturnix*), grey partridge (*P. perdix*), Eurasian thick-knee (*B. oedicnemus*), and little owl  
658 (*A. noctua*). The stock dove (*C. oenas*) and tawny owl (*S. aluco*) are associated with  
659 wooded areas, while the presence of the northern nutcracker (*N. caryocatactes*) suggests  
660 the presence of coniferous forests (Cramp, 1998) and confirms that, in the past, this  
661 species was distributed across a much broader area than today (Gala and Tagliacozzo,  
662 2010; Brichetti and Fracasso, 2011). The surroundings of Castelcivita were therefore  
663 characterised during MIS 3 by extensive wetlands in plain areas, and by drier  
664 environments (such as grasslands, bare terrains and cliffs) intermingled with conifer or  
665 mixed forests at higher elevations. The presence at about 100 m asl of species that  
666 currently live at higher altitudes (rock partridge, choughs and northern nutcracker),  
667 suggests colder and harsher conditions during the whole sequence. In the Uluzzian layer  
668 rpi, the number of bird taxa related to open environments increases and point to an  
669 expansion of grasslands linked to colder and more arid conditions possibly corresponding  
670 to the beginning of Heinrich Event 4 (or a preceding stadial), based on currently available  
671 dates (Fig. 8). In the Protoaurignacian layers, the riparian taxa slightly increase, as do  
672 those of forest environments in layer ars, probably indicating a climatic amelioration at the  
673 top of the sequence (Cassoli and Tagliacozzo, 1997; Gala et al., 2018). All phases  
674 provided evidence of human exploitation of at least some bird species (Fiore et al. in this  
675 issue).

676

FIGURE 8 HERE

### 4.3 Aoristic Analysis

As far as estimated relative frequencies of ungulates are concerned, the resulting graph exhibits trends of change over time (Fig. 9 B). The estimates of *Capreolus* relative abundance are high at 47.6 ky while they are increasingly lower at each step until ~44 ky. After ~45 ky the estimated remains of *Cervus elaphus* start becoming more abundant than in previous bins and reach their maximum between 44.6-43.6 ky. In bins following that date the presence of red deer starts declining in favour of *Capra ibex* and *Rupicapra rupicapra*. In the same time interval *Bos* and *Bison* show a quick unimodal trend. The apparent stability that emerges after ~40.5 ky it is due to the assumed uniform probability distribution in the absence of additional information on layer chronology. This trend, which can be noticed for all taxa, could be an artefact of uneven chronological sampling, and underscores the great temporal uncertainty associated with Protoaurignacian assemblages.

FIGURE 9 HERE

The distribution of relative carnivore estimates (Fig. 10) shows a marked increase in the presence of Ursidae between ~45 and ~43 ky. The relative frequency of wolves becomes higher than that of Ursidae between ~43.6 and 43.1 ky and becomes the highest value from 41.1 ky onwards. Foxes, on the other end, exhibit an opposite trend. From both an environmental and taphonomic point of view, it is interesting to note that after 41.1 ky the estimated relative frequency of *Crocuta crocuta spelaea* is considerably higher than in previous bins, including bins that record its presence between 47.6-46.6 ka.

701 FIGURE 10 HERE

702 Birds adapted to rocky environments are the most frequent at Fumane for the entire study  
703 sequence (Fig. 11). At 43.6 ky they exhibit a much lower estimate, while the percentage of  
704 avifaunal specimens linked to wooded/forested environments is higher at 43.6 ky than it  
705 was at the beginning of the sequence.

706 Rates of change based on simulated dates for ungulates (Figs. 9 and 11) add interesting  
707 elements and support this emerging scenario. When trends for ungulates are plotted  
708 against dummy sets based on estimated absolute frequencies of carnivores (i.e. of species  
709 with no particular links to change in environmental conditions), simulated 95% confidence  
710 envelopes exceed the expectations of the dummy model confidence area between 47.6-  
711 45.6 ky and 42-40.1 ky for bovids (Fig. 12 C), between 42 and 40.1 ky for caprids (Fig. 12  
712 B), while they only exceed the dummy model between 45.1-44.6 ky for cervids (Fig. 12 A)-.  
713 Although median values of simulated rates of change for all three ungulate families never  
714 emerge from the 95% dummy confidence envelope – suggesting the lack of significant  
715 deviations from a null model of deposition which is supposedly not based on  
716 environmental change – box-plots consistently point to the same chronological bins as the  
717 interesting ones. More specifically, there is evidence of a possible absolute increase in the  
718 frequency of all ungulate families between ~45.1-44.6 ky, while a decrease could be  
719 hypothesis between 44.6-43.6 ky.

720 Aoristic sum and simulated frequency estimates of all ungulates as a whole (Fig. 9 A)  
721 further support the hypothesis that at Grotta di Fumane there was an intensification of the  
722 deposition of ungulates between ca 45 and 43 ky, coinciding with higher percentages of  
723 red deer in the assemblages. A second moment of more intense process could be



identified between 41 and 39 ky, corresponding to higher percentages of *Capra ibex* and *Rupicapra rupicapra*. These trends confirm what emerged through the inspection of relative frequency estimates and of relative taxonomic abundance analysis, and hint at a potential change in environmental and climatic conditions in the region, but also point to a possible change in hunting and subsistence strategies, in particular by comparing ungulates, carnivores, and small preys from taxon abundance analysis.

FIGURE 11 HERE

FIGURE 12 HERE

#### 4.4 Human exploitation of mammals

The vast majority of faunal remains uncovered in Northeastern Italy (up to 97% in some contexts) is highly fragmented, i.e. with length comprised between 0.1 and 3 cm. Intense fragmentation in Northeastern contexts may be imputed to the marrow extraction activity and the use of fire, also to trampling and a set of natural processes (Tab. 2), but the potential influence of hyenas and other carnivores in specific layers (e.g. Grotta di Fumane USS A9-Mousterian, A3-Uluzzian, A2-Protoaurignacian; Tab. A.12) cannot be excluded, although, once estimated, it appears to be negligible. With the exception of Grotta del Rio Secco, burnt materials contribute to more than 50% of the total assemblage only in a few Late Mousterian contexts (Tab. 2). The proportion of calcined bones is higher in Uluzzian layers than in Late Mousterian ones. The frequency of butchering cut marks is also higher in the same temporal interval, while the frequency of percussion marks is lower across the

MP-UP transition (Tab. 3). In the same timeframe, most contexts exhibit higher numbers of cranial bones and limb extremities, and lower frequency of long bone fragments (Tab. 4). In contrast, elements of the trunk are underrepresented in the whole sequence on all contexts (Tab. 4).

751

TABLE 2 HERE

TABLE 3 HERE

754

All ungulate species bear traces of human exploitation (Fig. 12), and anthropic modifications were aimed at obtaining skin, meat, and marrow. The density of wear traces is higher on tibias, femurs and metapodials, radii, and humeri from cervids (red deer, roe deer, and very large specimens of giant deer or moose), and to a lesser extent on the same portions of other ungulates, many of which were likely used as retouchers (Jéquier et al., 2018; Romandini et al. 2018a).

At the end of the Middle Palaeolithic (Fumane A6, A5+A6; San Bernardino, Unit II), Ursidae (*Ursus spelaeus* and *Ursus arctos*) were heavily exploited for fur, meat and marrow, while red fox and beaver were hunted for their skins (Fig. 12). In the Uluzzian at Fumane (A3) there is clear evidence of skinning of foxes, *Canis lupus*, and *Ursus arctos*. (Tagliacozzo et al., 2013; Romandini, 2012; Romandini et al., 2014a, 2016a, 2018a, b). At the same site, the Protoaurignacian (A2) shows evidence of anthropic exploitation of all these carnivores (Fig. 12) with the addition of Eurasian lynx (*Lynx lynx*), while until now there is no evidence of exploitation of avifauna outside of the Mousterian and Uluzzian deposits (Peresani et al., 2011a; Tagliacozzo et al., 2013; Romandini et al., 2014b, 2016b; Fiore et al., 2004, 2016).

771

FIGURE 13 HERE

772 The southern Italian assemblages show the same high proportion of ungulates bearing  
773 traces of human exploitation as they do in northern Italy (Fig. 12). In addition, also in  
774 southern Italian contexts, the spectrum of hunted species mirrors coeval changes in  
775 climate and environment, and anthropic modifications are aimed at obtaining skins, meat,  
776 and marrow. It is interesting to note the low number of butchered small carnivores and  
777 lagomorph taxa, which are particularly concentrated in the Uluzzian and Protoaurignacian  
778 phases (Fig. 12). Grotta della Cala in southwestern/Tyrrhenian Italy exhibits increasingly  
779 higher percentages of phalanges and sesamoids across the Uluzzian, Protoaurignacian,  
780 Early Gravettian and Evolved Gravettian (Benini et al., 1997; Boscato et al., 1997, Boscato  
781 and Crezzini, 2007, 2012).

782

783 TABLE 4 HERE

784 TABLE 5 HERE

785 TABLE 6 HERE

786

787 Taphonomic analysis was carried out on a sample of identified ungulate remains from the  
788 Late Mousterian (NISP=67), Uluzzian (NISP=251), and Protoaurignacian (NISP=38) layers  
789 at Castelcivita (Southwestern Italy; Tab. 6). Specimens mostly consist of cranial and limb  
790 bones (especially metacarpals and metatarsals), while evidence of vertebral bones is  
791 limited. The frequency of small limb bones (phalanges, sesamoids, carpal, and tarsal) is  
792 higher in Uluzzian and Protoaurignacian layers than in Mousterian ones

793 (Mousterian=17.9%, Uluzzian=20.3%, Protoaurignacian=25%). The ratio of  
794 diaphysis/epiphysis fragments is lower in the Uluzzian and Protoaurignacian (4) than in the  
795 Late Mousterian (5.3). Anthropic marks were identified on 7.5% of remains in the Late  
796 Mousterian sample, on 10.6% of Uluzzian material, and have not been identified in the  
797 Protoaurignacian assemblage. Carnivore gnawing marks are fewer in the Protoaurignacian  
798 layers (2.6% of total material) and more abundant in the Late Mousterian (4.5%) and  
799 Uluzzian (7.7%) layers.

800 A sample of unidentified remains from the Mousterian levels of Castelcivita (n=1920) is  
801 highly fragmented (91.9% falls in the class 1-3 cm) (Tab. 5). In this context diaphysis  
802 fragments are the most abundant (40.4%), followed by spongy bones (16%), rib fragments  
803 (14.7%), and epiphysis fragments (7.2%) (Tab. A.10 and A.11). Anthropic marks are  
804 present on 2.8% of the unidentified material, while carnivores left traces on 1.5% of the  
805 remains (mostly vertebrae and epiphysis fragments).

806 As far as skeletal components of the most represented taxa are concerned (Tab. 7),  
807 results obtained at Castelcivita are consistent with what emerged from other southern  
808 contexts (Boscato and Crezzini, 2006, 2012), i.e. small limb bones (phalanges, sesamoids,  
809 carpal, and tarsal) and epiphyses are present with increasingly higher frequency across  
810 the archaeological sequence, while diaphysis fragments exhibit increasingly lower  
811 frequency (Tab. 7, A.10 and A.11). Nevertheless, the estimate of the contribution of  
812 anthropic actions to the formation of faunal assemblages found at Castelcivita may be  
813 biased by the presence of spotted hyena (*Crocuta crocuta spelaea*).

814 Most unidentified specimens fall in the smallest dimensional category (1-3cm), while the  
815 percentage of larger findings is higher in Uluzzian deposits (Tab. 5). Turning to  
816 Southeastern Italy, fragments of long bone diaphyses are abundant in the Mousterian

assemblages of Riparo l'Oscurusciuto and Grotta del Cavallo whereas epiphysis fragments are rare. At Grotta del Cavallo, on the other hand, percentages of diaphysis fragments are lower in the Uluzzian than they are in the Late Mousterian ones (Tab. A.11; Boscato and Crezzini 2006, 2012). Considering Riparo Oscurusciuto and Grotta del Cavallo (where bone assemblages are not biased by the action of carnivores), the observed differences between the Late Mousterian and the Uluzzian in the proportion of diaphysis, spongy-bone and phalanges are statistically significant (Tab. A. 15, A. 16, A. 17). As far as the degree of fragmentation is concerned, it is important not to directly compare any of the (preliminary) values currently available for Southern assemblages with those presented for the northern regions.

TABLE 7 HERE

## 5 Discussion

### 5.1 Comparison of taxon frequencies in macro-mammals between Northeastern, Southwestern, and Southeastern Italy

Mammal assemblages show that the Middle to Upper Palaeolithic Transition in Northern Italy was associated with a shift to colder and arid climatic conditions, as previously observed by Fiore et al. (2004) and Holt et al. (2019). In Northeastern Italy, human groups used rock shelters in the prealpine fringe and in the alpine foreland and exploited closed forest environments. The surroundings of such shelters were characterised by open environments, alpine meadows and cliffs populated by herbaceous and shrubby species,

841 while humans had to share and compete for their shelters with bears (Romandini et al.,  
842 2018a). At the end of Middle Palaeolithic, the examined faunal assemblages are  
843 dominated by cervidae while species adapted to open environments became considerably  
844 less abundant, suggesting a gradual change towards more temperate-humid climate which  
845 favoured the expansion of forests and wooded environments before the Uluzzian (such as  
846 in Fumane A4). Uluzzian and Protoaurignacian (e.g. Fumane A2) layers bear instead  
847 evidence of an abrupt shift to colder and arid conditions, which favoured the diffusion of  
848 steppic environments and alpine meadows. These observations are supported by the  
849 relative frequencies of cervids and caprines, both of which appear in higher percentages in  
850 moments of higher absolute intensity of deposition of ungulate remains. Caprids and  
851 bovids also show instances of increase and decrease that are not entirely predicted by the  
852 null model based on the distribution of carnivores (i.e. might actually be related to change  
853 in environmental conditions).

854 The aoristic analysis of Grotta di Fumane's zooarchaeological data confirm some of the  
855 trends observed by investigating taxon frequency across different sites of Northeastern  
856 Italy, especially in the first half of the study sequence. In addition, the comparison of  
857 simulated trends against null models based on constant deposition and on the aoristic sum  
858 of carnivores provides a means to more formally assess empirical patterns against explicit  
859 scenarios. This is particularly useful in a case study affected by small sample size and  
860 limited data comparability such as the present one. Most trends appear flattened in the  
861 aoristic sum graph, since the analysis explicitly incorporates the temporal uncertainty  
862 embedded in the present dataset. Nevertheless, the adoption of this approach paves the  
863 ground for future direct comparisons between northern and southern contexts by  
864 highlighting long-term processes that can be directly compared against palaeoecological

865 and paleoclimatic data collected from a variety of archives, so that future inferences on  
866 change in adaptive strategies can be more objective. Additional dates and more detailed  
867 information on taphonomy and post-depositional processes will also help shed light on the  
868 mechanisms actually underlying the potential diachronic change for Protoaurignacian  
869 contexts.

870 In southern Italy, Late Mousterian deposits exhibit evidence of generally temperate  
871 conditions. In this phase, cervids are the most common ungulates in the Tyrrhenian region,  
872 while *Bos primigenius* is the most represented species in Ionian contexts. At Grotta di  
873 Castelcivita, this phase is characterised by the same palaeoenvironmental trend  
874 documented at Fumane.

875 The Uluzzian phases at Grotta del Cavallo and Grotta di Castelcivita show data compatible  
876 with the establishment of a colder climate, while human groups active at Grotta della Cala  
877 experienced more temperate conditions. During MIS 3, the Tyrrhenian side appears to be  
878 still characterised by temperate and humid conditions favouring forests and wooded  
879 environments, while the Ionian areas were marked by steppic environments and wooded  
880 steppe.

881 Outside of the Italian Peninsula, the only possible comparisons in terms of temporal span  
882 and of an archaeological sequence comprising Late Mousterian – Uluzzian –  
883 Protoaurignacian (only Aurignacian in Greece) It's represented by Kephalaria and Klissoura  
884 Cave, Peloponnese, Greece (Starkovich, 2012; Starkovich and Ntinou, 2017; Starkovich et  
885 al., 2018). Especially at the latter site, the MIS 3 was highly variable, as suggested by  
886 evidence of variation between forested environments, mixed forest-steppe (with red deer,  
887 roe deer, chamois and ibex), and drier intervals with steppe species such as European  
888 wild ass, aurochs, ibex and great bustard. Fallow deer, tortoises, European hare, and rock

889 partridges also are well adapted to all these environments regimes. The Uluzzian (V) and  
890 Aurignacian (IV) layers yielded evidence of Fallow deer and small game, in addition to  
891 species adapted to both open and forested environments. Plants indicate a mixture of  
892 forest and steppe, although taxonomic evenness suggests that conditions were slightly  
893 wetter in the Uluzzian layers than during the final MP occupations.

894 If we exclude Upper Palaeolithic layers of both Kephalaria and Klissoura Cave, the  
895 exploitation of small game across the transition between Middle and Upper Palaeolithic  
896 could be linked to coeval environmental change and a change in resource availability, as it  
897 is suggested by the remains of tortoise and hare identified at Klissoura Cave<sup>1</sup> in  
898 assemblages associated with Neandertals (Starkovic et al 2012; 2017, 2018). The range  
899 of hunted taxa in this region therefore seems to be stable across the Middle and Upper  
900 Palaeolithic, and trends can be ascribed to species availability dictated by environmental  
901 and climatic change, rather than to convergence in hunting strategies with the Italian  
902 Peninsula (Starkovich et. al. 2018). At present a more detailed comparison between the  
903 exploitation of animal remains documented in Italy and Greece is not yet possible as  
904 research on the subject is still in progress and additional data are required. Nevertheless,  
905 trends emerging from taxon abundance analysis are broadly comparable to those  
906 identified for Southwestern and Southeastern Italy and documented in the present work.

907 On the other hand, preliminary results presented here suggest in Middle to UP transition a  
908 more intensive exploitation of small game in Northeastern Italy than in Southern contexts  
909 and the Peloponnese. This finding might be particularly relevant for interpreting regional  
910 patterns of change in subsistence/adaptive strategies, considering that large game is  
911 generally considered a higher-rank resource than small game.

912



## 913 **5.2. Comparison of avifaunal remains between Fumane and Castelcivita**

914 The avifaunal assemblages of Grotta di Fumane and Grotta di Castelcivita provide  
915 relevant insights on the paleoenvironmental and paleoclimatic framework of both deposits.  
916 The surroundings of Fumane were characterised by mixed and conifer forests, grasslands  
917 and alpine meadows with rocky outcrops, cliffs and slow-flowing water bodies. The  
918 environmental framework of Grotta di Castelcivita was instead characterised by wetlands  
919 in the plains in front of the cave and by drier habitats like grasslands, rocky terrains and  
920 rock walls, alternated to conifer or mixed forests at higher altitudes.

921 Bird taxa across Italy indicate the presence of a consistently colder climate than the  
922 present one. Nevertheless, in the southwestern/Tyrrhenian area (Fig. 1, Area 2) climate  
923 seems milder and more temperate than in the Adriatic area, as suggested by the absence  
924 of boreal bird species and by a lower proportion of high altitude bird taxa in the former.

925 Once again, faunal assemblages mirror climatic differences between Tyrrhenian and  
926 Ionian/Adriatic regions mostly due to the effect of the Balkanic influence on the latter. The  
927 Middle Paleolithic assemblages from both sites provide evidence of temperate-cool  
928 climate, where the species of open and rocky habitats prevail. The Late Mousterian Layer  
929 A6 at Fumane hints at a possible cold oscillation, however, and the Uluzzian at both sites  
930 (A3 at Grotta di Fumane, and CTC rsi at Grotta di Castelcivita) shows higher percentages  
931 of bird taxa typical of open habitats possibly due to colder conditions linked to Heinrich  
932 Event 4 (Higham et al., 2009; Moroni et al., 2018; Lopéz-García et al., 2015).

933 Protoaurignacian deposits provide evidence for the persistence of harsh conditions which  
934 characterized previous phases. In spite of the low NISP, one exception seems to be  
935 represented by the latest Protoaurignacian layers of Castelcivita (gic-ars; referring here  
936 particularly to the layer ars, as the bird bone sample of the layer gic was too small to

include it in the analysis), that yielded evidence for climatic shift toward more humid conditions (Cassoli and Tagliacozzo, 1994b, 1997; Gala et al., 2018).

### 5.3 Taphonomy

Despite the facts that taphonomic data are still only partially investigated in most of the sampled contexts and that the majority of identified patterns cannot be proven to be statistically significant because of small sample size, interesting preliminary trends emerge. Although future studies may alter the pattern detected so far, at present, the percentage of calcined remains during the Uluzzian and Protoaurignacian levels in Northeastern Italian contexts is higher than the frequency of the same items in previous phases, and hints at a possible behavioural change linked to the use of fire: greater intensity and duration of use of the hearths, differentiation of fuel and/or cooking of animal resources. Cut-marks are also more frequent across the transition, while the degree of bone fragmentation for marrow extraction is higher in Mousterian layers than in later deposits. In the Early Upper Palaeolithic overall (i.e., Uluzzian and Protoaurignacian) there are higher percentages of cranial bones and limb extremities, with a consequent lower proportion of long bones. This trend may be imputed partly to human selection and partly to the use of the cave by hyenas and other carnivores. The remains of the most frequently hunted large (Cervidae, Bovinae) and medium-sized (Caprinae) ungulates show cut- and percussion-marks, all of which point to skinning, butchering, and marrow extraction. Over the same timespan, bears and middle- and small-sized carnivores appear to be more frequently exploited, suggesting a broadening in the range of species hunted for skin and fur (Collard et al., 2016).

960 Avifaunal assemblages provide evidence of human consumption of birds and contribute to  
961 an understanding of the role of avifaunal resources in the subsistence strategies of Middle  
962 Palaeolithic hominins (Peresani et al., 2011a; Romandini, 2012; Tagliacozzo et al., 2013;  
963 Fiore et al., 2016; Romandini et al., 2014b; 2016a, b; Gala et al., 2018; Fiore et al., in this  
964 issue). The exploitation of these resources is testified by recognizable taphonomic  
965 indicators such as evidence for the exploitation of feathers from various raptors and other  
966 birds.

967 In the same way, evidence of Neandertal reliance on small mammal prey increased over  
968 the past 10 years due to the reassessment of faunal assemblages from a new taphonomic  
969 perspective (Romandini et al., 2018b; Morin et al., 2019).

970 In Ionian contexts, Late Mousterian assemblages exhibit a lack (or at least a scarcity) of  
971 long-bone epiphyses, carpal and tarsal bones, phalanges and sesamoides. In the  
972 analysed Late Mousterian samples from Grotta del Cavallo and Riparo l'Oscurusciuto, this  
973 evidence cannot be attributed to carnivores, differential bone density and other post-  
974 depositional processes (Boscato and Crezzini, 2006, 2012). The frequency of different  
975 anatomical parts (% of Minimum Animal Units, Binford, 1984) of *Bos primigenius* and the  
976 modal species in US 4 at Riparo l'Oscurusciuto were compared against Emerson's utility  
977 indices related to present-day *Bison bison* (Emerson, 1990, 1993). Previous results  
978 suggest a relationship between bone frequency and their content in marrow and fat, which  
979 was probably crucial in the choice to select specific anatomical parts and to carry them  
980 back to camps/sites (Boscato and Crezzini, 2006, 2012). Recent studies demonstrated  
981 that at least at Riparo l'Oscurusciuto spongy bones were not systematically used as fuel in  
982 hearths (Spagnolo et al., 2016), suggesting their possible use as food (Costamagno and  
983 Rigaud, 2014). In southern Italy, Upper Palaeolithic assemblages indicate a different

manner of exploiting ungulate bones (Boscato and Crezzini, 2006, 2012). A large amount of long-bone epiphyses and spongy elements (including carpal and tarsal bones) were not destroyed and can be found in these assemblages. Unlike Neandertals, who were evidently not interested in phalanges and probably left them at the kill sites, modern humans usually transported these small skeletal parts to their campsites where they fragmented them to recover the particular fat they contained: Morin (2006) underlines that, although the phalanges contain a low quantity of marrow, it is qualitatively different than the marrow contained in long bones, due to its higher percentage of oleic acid. These data suggest a change in processing hard animal tissues by Upper Palaeolithic people across southern Italy, a change that is already visible in Uluzzian assemblages, as documented by the case of Layer EIII5 at Grotta del Cavallo (Boscato and Crezzini, 2006, 2012).

## 6 Conclusions

The data collected and analysed to date show that human adaptive strategies changed over time to cope with variability in local topographic and ecological conditions, as well as with uncertainty in resource availability. Uncertainty and bias are critically embedded in the procurement and treatment of animal resources, especially in such a fragmented and small-scale scenario as the Italian Peninsula. A sample of key sites from both southern and northern Italy offers rich evidence of how groups of Neandertals and modern humans occupied the Tyrrhenian and Ionian areas, as well as through the area between the great alluvial plain of the river Po and the Pre-Alpine mountains. In this context, a thorough and detailed zooarchaeological approach offers a unique perspective on palaeoenvironmental and palaeoecological settings, as well as on hunting and subsistence strategies. In the present study, we presented state-of-the-art evidence on the differential presence of large

mammals and avifauna across Late Mousterian, Uluzzian, and Protoaurignacian assemblages from Italy. Incorporating an aoristic analysis further allows us to explicitly address the amount of temporal uncertainty embedded in one of the zooarchaeological assemblages of interest. While losing detail on individual archaeological layers, this method offers a practical solution to help overcome the effects of time-averaging and of the lack of information on layer-specific accumulation rates. At the same time, aoristic sums for ungulates, rates of change based on simulated data, and the comparison with null models depict a conservative scenario useful for inferring instances of *absolute* increase or decline of given taxa or families over time. The analysis of environmentally-informative bird taxa added significant detail to the environmental trends provided by mammal remains, improving our understanding of the climatic framework of the Middle-Upper Paleolithic transition. The future addition of micromammals to the analysis will make it possible to add detail on local biotopes, and to further test inferences on palaeoclimatic change in the different contexts. Interesting hypotheses on human behavioural ecology also emerge from the examined archaeological assemblages, although additional evidence is still clearly required for objectively test inferences about Uluzzian and Protoaurignacian contexts. In particular, differences seem to emerge in the use of fire (especially in terms of temperatures and bone processing) between Late Mousterian layers and the subsequent phases. More substantial data on the distribution of ungulate limb elements suggest a marked change in prey exploitation between the Late Mousterian and the Early Upper Palaeolithic in southern Italy, while northern sites show that a higher variety of processing techniques was already present in the Late Mousterian. As concerns differences in hunting strategies, traces of an increasing preference for small- and medium-sized mammals (carnivores, rodents, lagomorphs) can be already documented for

1032 the transition to Protoaurignacian, although presently available evidence is exclusively  
1033 qualitative. Future research will ascertain if this difference can be ascribed to a forced  
1034 expansion of niche breadth due to economic and technological competition between  
1035 Neandertals and modern humans (Hockett and Haws 2005).

1036 The above mentioned hypotheses cannot yet be tested because of small sample size in all  
1037 the analysed classes, and the emerging trends may or may not be confirmed by adding  
1038 evidence on the same sites as well as on other, currently underrepresented areas of the  
1039 Italian Peninsula to the analyses presented here. Over the next three years, the project  
1040 ERC n. 724046 – SUCCESS will build on the results presented here by acquiring novel  
1041 zooarchaeological and chronological evidence on all the mentioned contexts (Fig. 1), by  
1042 directly comparing faunal time series to palaeoenvironmental and palaeoclimatic data, and  
1043 by relying on innovative methods (Pothier Bouchard et al., 2019; Pothier Bouchard et al.,  
1044 this issue) such as ZooMS (ZooArchaeology by Mass Spectrometry). This evidence will  
1045 contribute to helping resolve or at least clarify longstanding debates surrounding strategic  
1046 and technological shifts which occurred during the Middle-Upper Paleolithic transition and  
1047 will help situate the questions concerning contacts between Neandertals and modern  
1048 humans in Italy (and the eventual replacement of the former by the latter) in the broader  
1049 framework of complex adaptive strategies and long-term human-environment interactions.

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1077

1078 **Data Availability**

Datasets, scripts and related commands used to generate all of the results described in the paper are available at (<http://doi.org/10.6092/unibo/amsacta/6209>).

## Captions

### Figure captions

Figure 1: MIS 3 map of Italy (modified from Moroni et al., 2018) and the geographic location of the sites with previously published faunal assemblages mentioned in this work and dated between ca. 50 and 38 ky ago. Sites that are part of the project ERC n. 724046 – SUCCESS are numbered from 1 to 10. Sites analysed in this work are assigned numbers 1-8, and are located in study Areas 1-3 (Northeastern, Southwestern/Tyrrhenian, and Southeastern/Ionian respectively). For each sites the colors represent the presence of levels, USS and/or layers chronologically and technologically linked respectively to the Protoaurignacian = blue; Uluzzian =yellow; Late Mousterian = red. 1) Grotta del Rio Secco; 2) Riparo del Broion; 3) Grotta di San Bernardino; 4) Grotta di Fumane; 5) Riparo Bombrini; 6) Grotta di Castelcivita; 7) Grotta della Cala; 8) Riparo l'Oscurusciuto; 9) Grotta del Cavallo; 10) Grotta di Uluzzo C; 11) Riparo Mochi; 12) Grotta del Principe; 13) Grotta dell'Observatoire; 14) Arma delle Manie; 15) Arma degli Zerbi; 16) Buca della Iena; 17) Grotta la Fabbrica; 18) Grotta dei Santi; 19) Grotta Breuil; 20) Grotta del Fossellone; 21) Grotta S. Agostino; 22) Grotta Reali; 23) Riparo del Poggio. The Italian Peninsula shows a sea level of 70 m below the present-day coastline, based on the global sea-level curve (Benjamin et al., 2017) but lacking the estimation of post-MIS3 sedimentary thickness and eustatic magnitude (sketch map courtesy by S. Ricci, University of Siena).



1102 Figure 2: % comparison of the NISP of Ungulata, Carnivora, Rodentia-Lagomorpha and  
 1103 birds (the latter only for Grotta di Fumane and Castelcivita) of the sites being analysed  
 1104 (Fig. 1) divided by macro-geographical area and cultural phases: LM = Late Mousterian;  
 1105 UL = Uluzzian; PA = Protoaurignacian.

1106 Figure 3: Northern Italy sites; simple histograms, % comparison of the ungulates taxa,  
 1107 calculated on the ungulates Total Nisp, in the different levels and layers in chronological  
 1108 order based on the archaeological sequence. RF = Grotta di Fumane; RB = Riparo del  
 1109 Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. LM = Late Mousterian;  
 1110 UL = Uluzzian; PA = Protoaurignacian.

1111 Figure 4: Northern Italy sites; simple histograms, % comparison of the carnivores taxa,  
 1112 calculated on the carnivores Total Nisp, in the different levels and layers in chronological  
 1113 order based on the archaeological sequence. RF = Grotta di Fumane; RB = Riparo del  
 1114 Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. LM = Late Mousterian;  
 1115 UL = Uluzzian; PA = Protoaurignacian.

1116 Figure 5: Southern Italy Tyrrhenian area sites; simple histograms % comparison of the  
 1117 ungulate taxa, calculated on the ungulate Total Nisp, in the different levels and layers in  
 1118 chronological order based on the archaeological sequence; CTC = Grotta di Castelcivita;  
 1119 CALA = Grotta della Cala. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

1120 Figure 6: Southern Italy, Ionian-Adriatic area sites; simple histograms, % comparison of  
 1121 the ungulate taxa, calculated on the ungulate Total Nisp, in the different levels and layers  
 1122 in chronological order based on the archaeological sequence. CAV = Grotta del Cavallo;  
 1123 OSC = Riparo l'Oscurusciuto. LM = Late Mousterian; UL = Uluzzian; PA =  
 1124 Protoaurignacian.

Figure 7: % share of the bird taxa of different environments (see legend) in the various layers of Grotta di Fumane, calculated on the total number of bird taxa of each layer. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

Figure 8: % share of the bird taxa of different environments (see legend) in the various layers of Grotta di Castelvita, calculated on the total number of bird taxa of each layer. LM = Late Mousterian; UL = Uluzzian; PA = Protoaurignacian.

Figure 9: A) Aoristic sum and estimated chronological frequency distribution of ungulates at Grotta di Fumane. The solid black line represents the aoristic sum, while the darker grey polygon indicates the simulated 95% confidence interval. The dark grey solid line-and-dots corresponds to simulated median values. The lighter grey envelope is instead the 95% confidence region of the null model based on uniform frequency distribution across the entire study period; B) Estimated diachronic relative frequency of each ungulate taxon based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP.

Figure 10: Estimated diachronic relative frequency of each carnivore taxon at Grotta di Fumane, based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP..

Figure 11: Estimated diachronic relative frequency of avifaunal remains grouped by the relative environment, based on aoristic sums computed for 500-year temporal bins. Horizontal axis indicates dates cal. BP..

Figure 12: Simulated diachronic rates of change computed for ungulate families at Grotta di Fumane. Box-plots and coloured polygons indicate the distribution of simulated rates of change based on observed family frequencies, while grey polygons represent 95% confidence regions for a null model based on the aoristic sums of carnivores uncovered at

the same archaeological site. A (green): Cervidae; B (blue): Caprinae; C (red): Bovinae. Based on 5000 simulation runs and computed at 500-year bin resolution.

Figure 13: A) Northern Italy sites, comparative summary trend scheme of the different cultural phases, representing the taxa whose bones bear cut-marks, percussion marks or are burned. RF = Grotta di Fumane; RB = Riparo del Broion; GSB = Grotta di San Bernardino; RS = Grotta del Rio Secco. B) Southern Italy sites. CAV = Grotta del Cavallo; OSC = Riparo l'Oscurusciuto; CTC = Grotta di Castelvita; CA = Grotta della Cala. Legend color: Protoaurignacian = blue; Uluzzian = yellow; Late Mousterian = red.

#### Tables captions

Table 1: detailed context table of sites analysed in this work.

Table 2: different size classes of mammals bones and burned remains with relative %, identified in the MP/UP transition from the Northern Italy sites (see Fig. 1 - Area 1). RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

Table 3: number of remains (NR) and relative % with anthropic modifications identified in the MP / UP transition from the Northern Italy sites (see Fig.1 - Area 1). RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco. CM = Cut Marks; SCR.= Scrapings; IF= Impact Flakes; PM= Percussion Marks; BM = Butchering Marks.

Table 4: number of remains and relative % of the specific anatomical elements, referring to the most represented mammals species present in the layers and levels from MP/UP transition Northern Italy sites (see Fig. 1 – Area 1). Below, the subtotals of the different

1172 anatomical compartments. RF = Grotta di Fumane; RB = Riparo del Broion; SB = Grotta di  
 1173 San Bernardino; RS = Grotta del Rio Secco.

1174 Table 5: different size classes of mammals bones and burned remains (NR) with relative  
 1175 %, identified in the LM and UL layers from the Southern Italy sites (see Fig. 1 – Area 2+3).  
 1176 CAV = Grotta del Cavallo; CTC = Grotta di Castelvita; OSC = Grotta l'Oscurusciuto.

1177 Table 6: number of remains (NR) and relative % with anthropic modification identified in  
 1178 the MP/UP transition from the Southern Italy sites (see Fig. 1 – Area 2+3). CAV = Grotta  
 1179 del Cavallo; OSC = Riparo l'Oscurusciuto; CTC = Grotta di Castelvita. CM = Cut Marks ;  
 1180 SCR.= Scrapings ; IF= Impact Flakes ; PM= Percussion Marks ; BM = Butchering Marks.

1181 Table 7: number of remains and relative % of the specific anatomical elements, referring to  
 1182 the most represented mammal species present in the layers and levels from MP/ UP  
 1183 transition Southern Italy sites (see Fig. 1 – Area 2+3). Below are the subtotals of the  
 1184 different anatomical compartments. CAV = Grotta del Cavallo; OSC = Riparo  
 1185 l'Oscurusciuto; CTC = Grotta di Castelvita; CALA = Grotta della Cala.

1186

#### 1187 **Table captions appendices**

1188 Table A.1: levels and layers of the Northern Italy sites in chronological-cultural order  
 1189 (Adriatic area). Detail of Ungulata Total Nisp and relative %. RF = Grotta di Fumane; RB =  
 1190 Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

1191 Table A.2: levels and layers of the Northern Italy sites in chronological-cultural order  
 1192 (Adriatic area). Detail of carnivore Total Nisp and relative %. RF = Grotta di Fumane; RB =  
 1193 Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio Secco.

1194 Table A.3: levels and layers of the Northern Italy sites in chronological-cultural order  
 1195 (Adriatic Area 1 in Fig. 1). Detail of Rodentia and Lagomorpha Total Nisp. RF = Grotta di

1196 Fumane; RB = Riparo del Broion; SB = Grotta di San Bernardino; RS = Grotta del Rio  
 1197 Secco.

1198 Table A.4: levels and layers of the South Italy Tyrrhenian sites (Area 2 in Fig.1) in cultural  
 1199 order. Detail of Ungulata Total Nisp and relative %. CTC = Grotta di Castelcivita; CALA =  
 1200 Grotta della Cala.

1201 Table A.5: levels and layers of the South Italy Tyrrhenian sites (Area 2 in Fig. 1) in cultural  
 1202 order. Detail of Carnivora Total Nisp. CTC = Grotta di Castelcivita; CALA = Grotta della  
 1203 Cala.

1204 Table A.6: levels and layers of the South Italy Ionian-Adriatic sites (Area 3 in Fig. 1) in  
 1205 cultural order. Detail of Ungulata Total Nisp and relative %. CAV = Grotta del Cavallo;  
 1206 OSC = Riparo l'Oscurusciuto.

1207 Table A.7: levels and layers of the South Italy Ionian-Adriatic sites (Area 3 in Fig.1) in  
 1208 cultural order. Detail of Carnivora Total Nisp. CAV = Grotta del Cavallo; OSC = Riparo  
 1209 l'Oscurusciuto.

1210 Table A.8: Nisp and relative % of the avifaunal taxa recovered in different levels and layers  
 1211 of Grotta di Fumane and Grotta di Castelcivita, in chronological-cultural order. For the  
 1212 taxonomic order, we followed Del Hoyo et al., 2014 and 2016.

1213 Table A.9: Starting and Ending dates for each of the archaeological layers used in aoristic  
 1214 analysis. These dates were either obtained directly from relevant literature or, when more  
 1215 dates for the same layer were available, by taking the upper and lower limits of the  
 1216 summed probability distribution of dates after calibration thought rcarbon in R (Bevan and  
 1217 Crema, 2018) using Intcal13 calibration curve (Reimer et al., 2013).

1218 Table A.10: number and % of single teeth and small limb bones of Ungulata from different  
 1219 levels of the Late Mousterian, Uluzzian and Protoaurignacian Southern Italy sites. CALA =

1220 Grotta della Cala; CTC = Grotta di Castelcivita; CAV = Grotta del Cavallo; OSC = Riparo  
 1221 l'Oscurusciuto.

1222 Table A.11: percentages of determinated skeletal parts in the taxonomically indeterminate  
 1223 remains recovered from the different Late Mousterian and Uluzzian layers and levels of the  
 1224 Southern Italy sites. OSC = Riparo l'Oscurusciuto; CAV = Grotta del Cavallo; CTC = Grotta  
 1225 di Castelcivita.

1226 Table A.12: levels and layers of the Northern Italy sites in chronological-cultural order  
 1227 (Adriatic Area 1 in Fig. 1). Detail and relative percentages of digested and gnawing  
 1228 remains by carnivore. GM: gnawing marks; TOT CM: total carnivore marks; D: digested.

1229 Table A.13: Results of Mann-Whitney test for assessing significant differences in the  
 1230 distribution of fragment size classes and the proportion of burned and calcinated remains  
 1231 across Uluzzian and Late Mousterian layers of Northern Italy. The test was run on arcsine-  
 1232 transformed proportions.

1233 Table A.14: Results of test for differences in proportion of fragment size classes between  
 1234 Uluzzian and Late Mousterian layers of southeastern Italy (i.e. those with no direct  
 1235 evidence of carnivore gnawing) with relative effect size and statistical power.

1236 Table A.15: Results of test for differences in proportion of carpal/tarsal and  
 1237 phalanges/sesamoides of *Bos primigenius* between Uluzzian and Late Mousterian layers  
 1238 of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with the  
 1239 relative effect size and statistical power.

1240 Table A.16: Results of test for differences in proportion of carpal/tarsal and  
 1241 phalanges/sesamoides across all ungulates between Uluzzian and Late Mousterian layers  
 1242 of southeastern Italy (i.e. those with no direct evidence of carnivore gnawing) with the  
 1243 relative effect size and statistical power.

1244 Table A.17: Results of test for differences in proportion of diaphysis, epiphysis, and  
1245 spongy bones between Uluzzian and Late Mousterian layers of southeastern Italy (i.e.  
1246 those with no direct evidence of carnivore gnawing) with the relative effect size and  
1247 statistical power.

1248

1249 Figure A.1: Plot of individual calibrated dates (with the IntCal13 curve) and of posterior  
1250 probability of phase boundaries determined using the overlapping phase bayesian model  
1251 in OxCal 4.3 (Bronk Ramsey 2009, 2017).

1252 Figure A.2: Bayesian model for Grotta di Fumane (A9-A2) produced with OxCal 4.3 (Bronk  
1253 Ramsey 2009, 2017) using only ABOx-SC dates on charcoal and ultrafiltered bone dates  
1254 available in the literature (Higham 2009, Higham 2011, Douka et al. 2014). Individual date  
1255 likelihoods are shown in light grey, while posterior probability distributions are shown in  
1256 dark grey. The medians of the posterior distributions of phase boundaries were taken as  
1257 layer start/end dates to be used in aoristic analysis.

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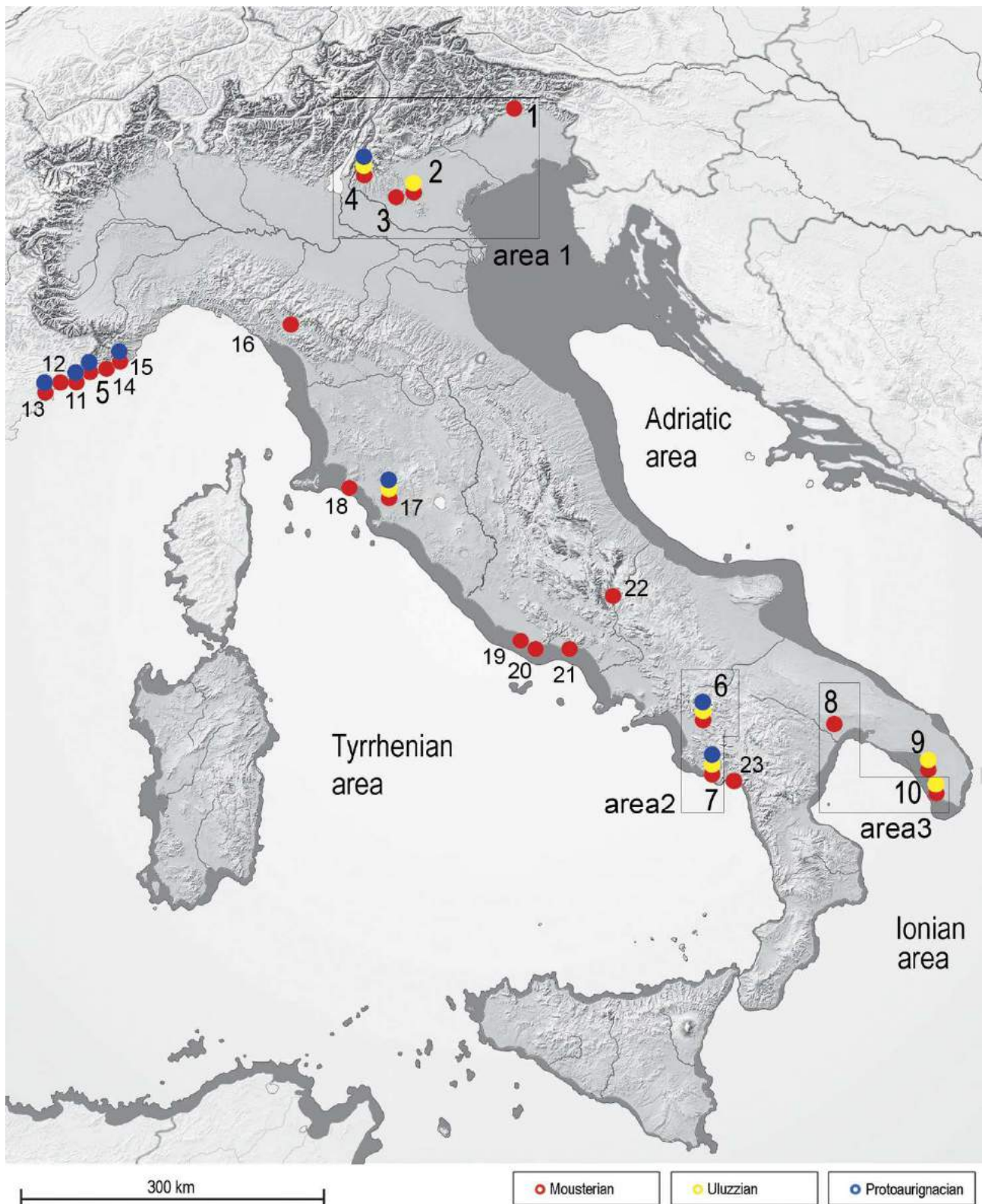
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1266 *Figure 1*



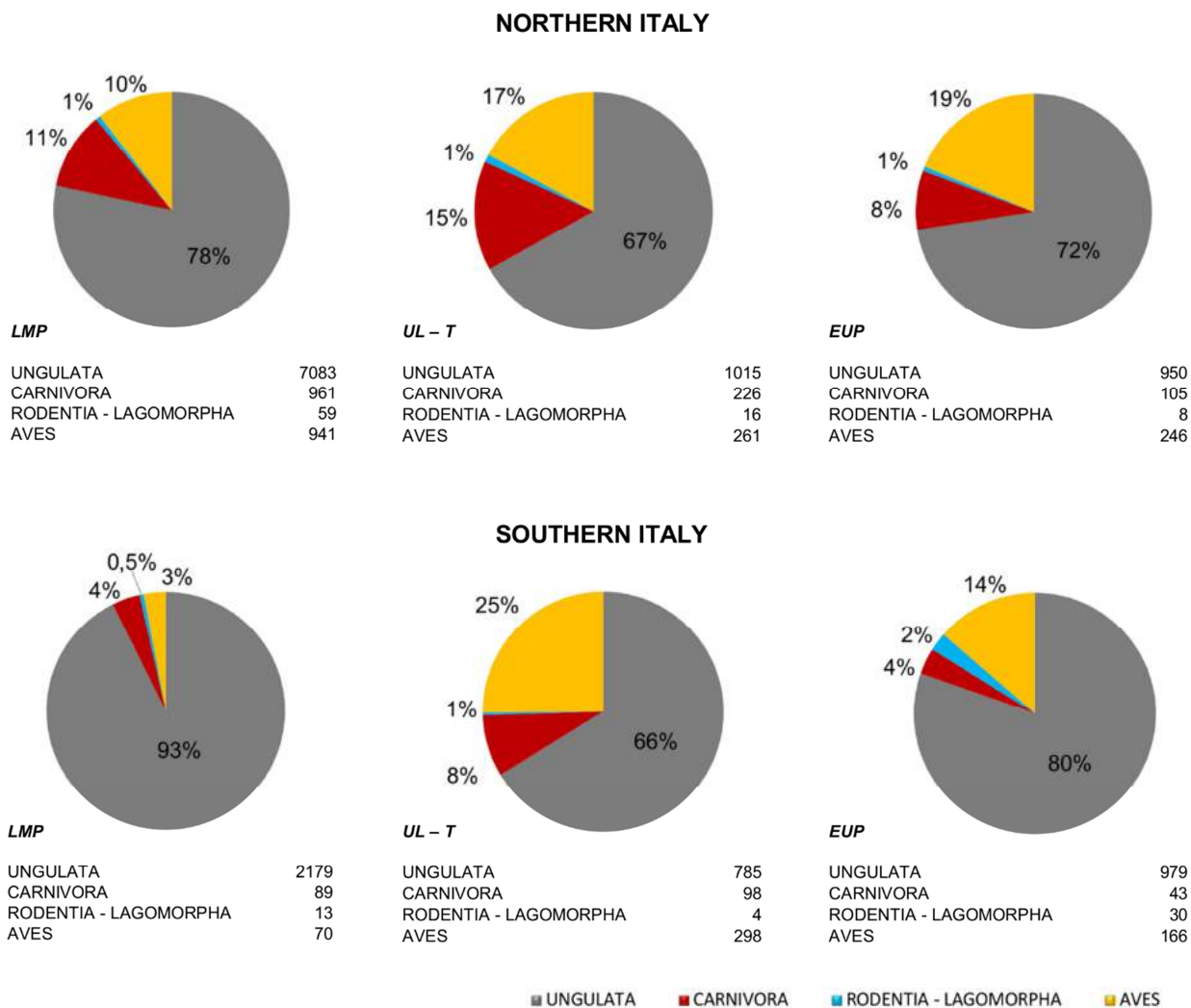
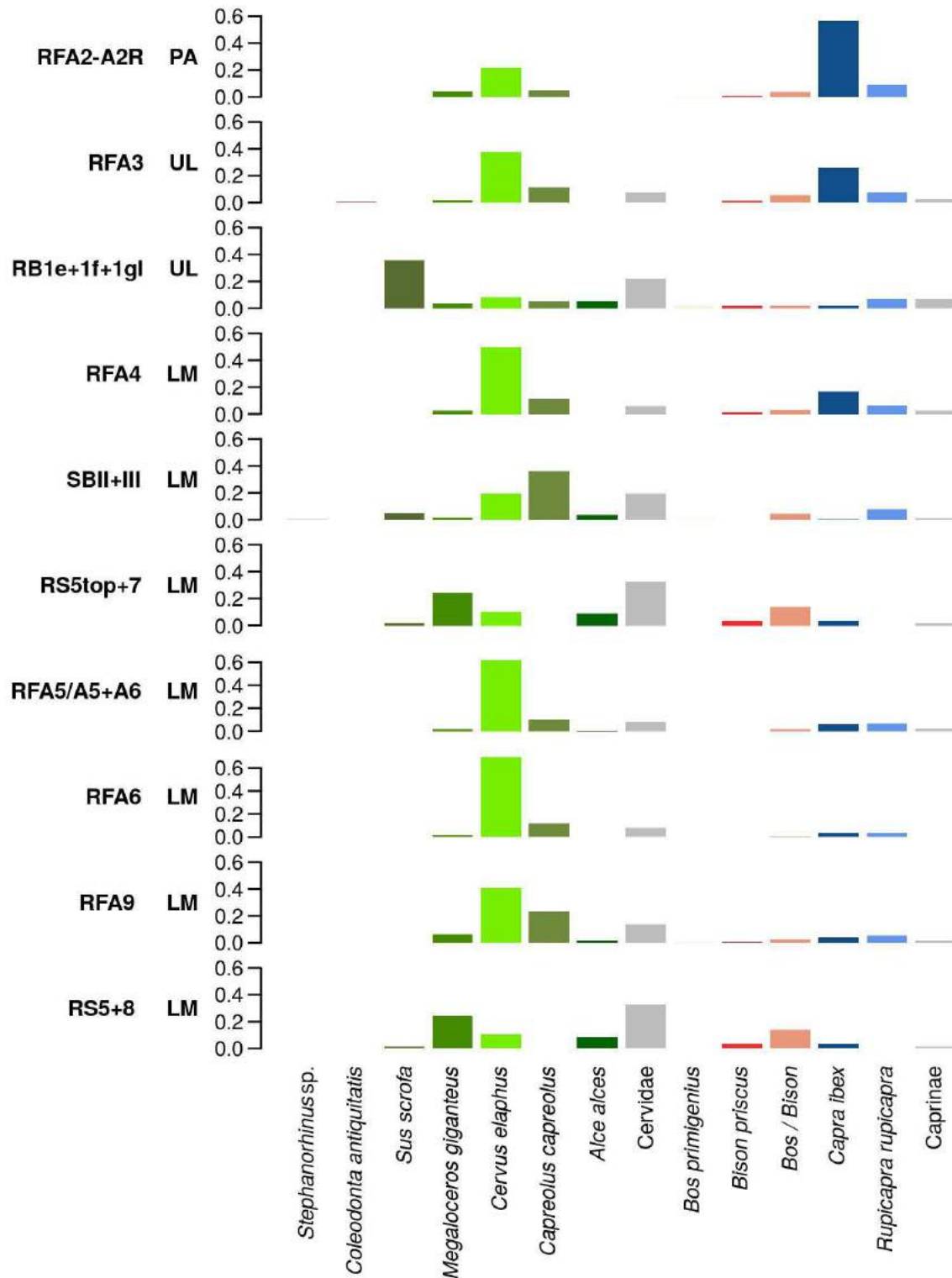
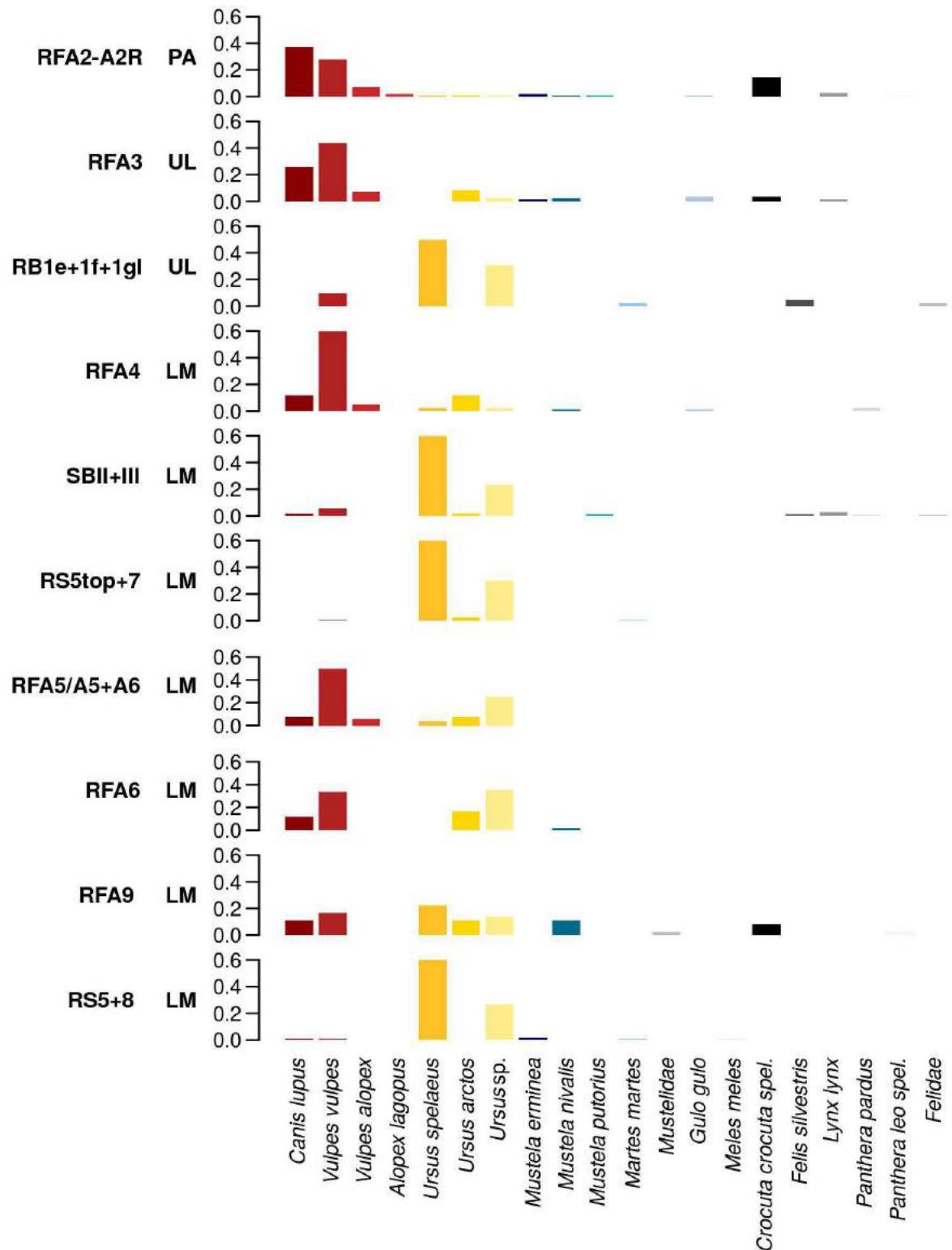


Figure 2



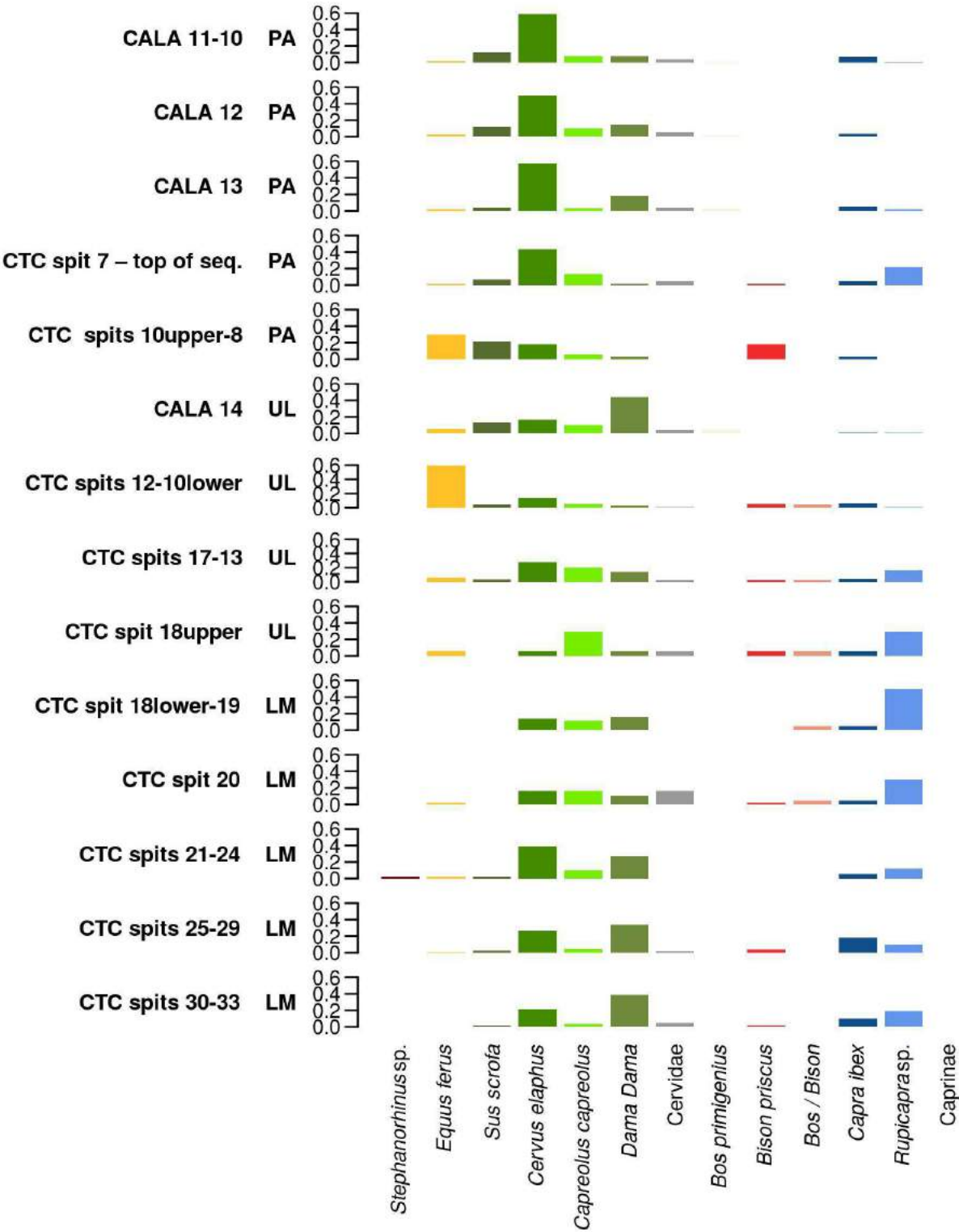
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1270 Figure 3



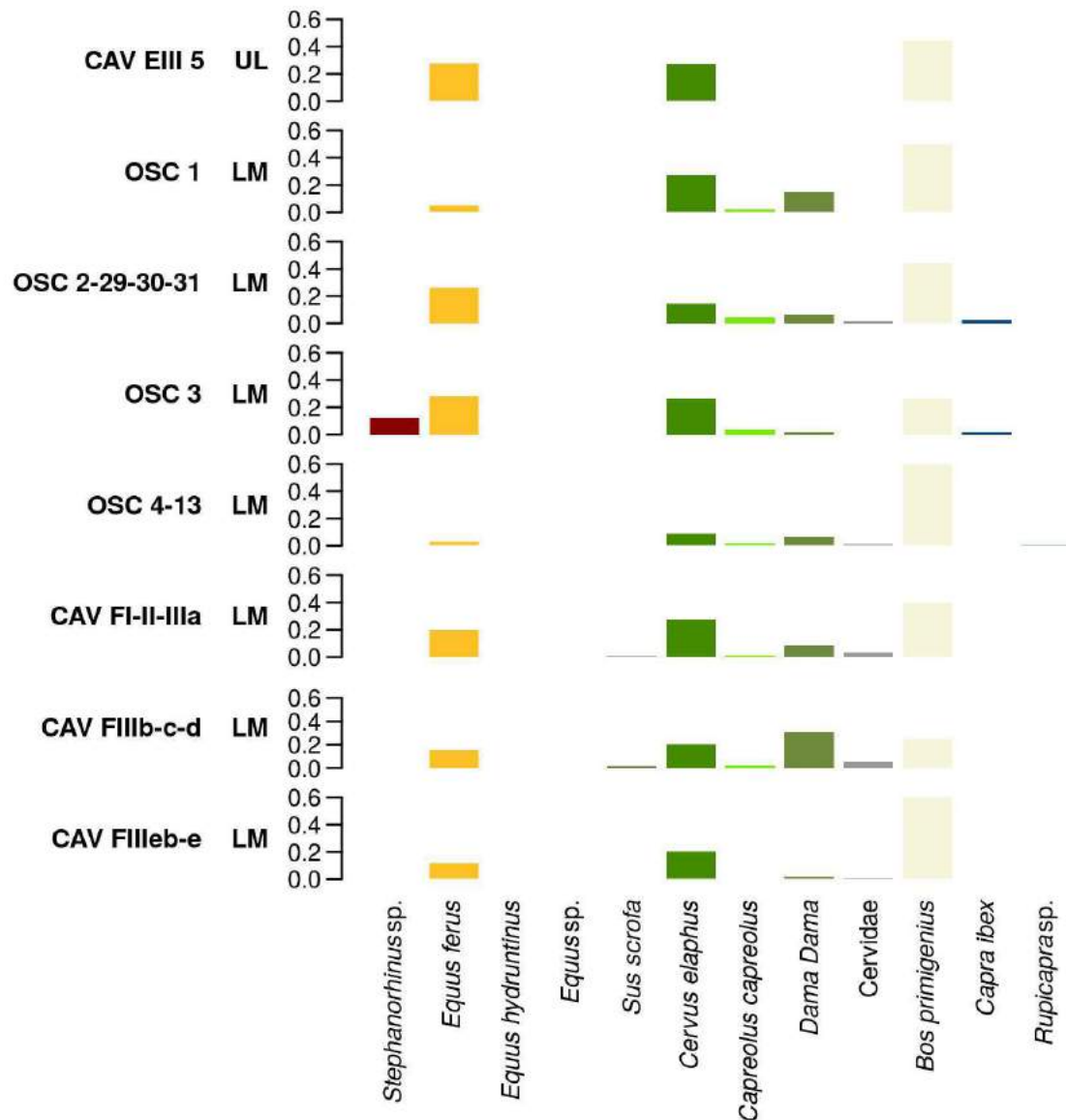
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1272 Figure 4



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1274 Figure 5



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1276 Figure 6

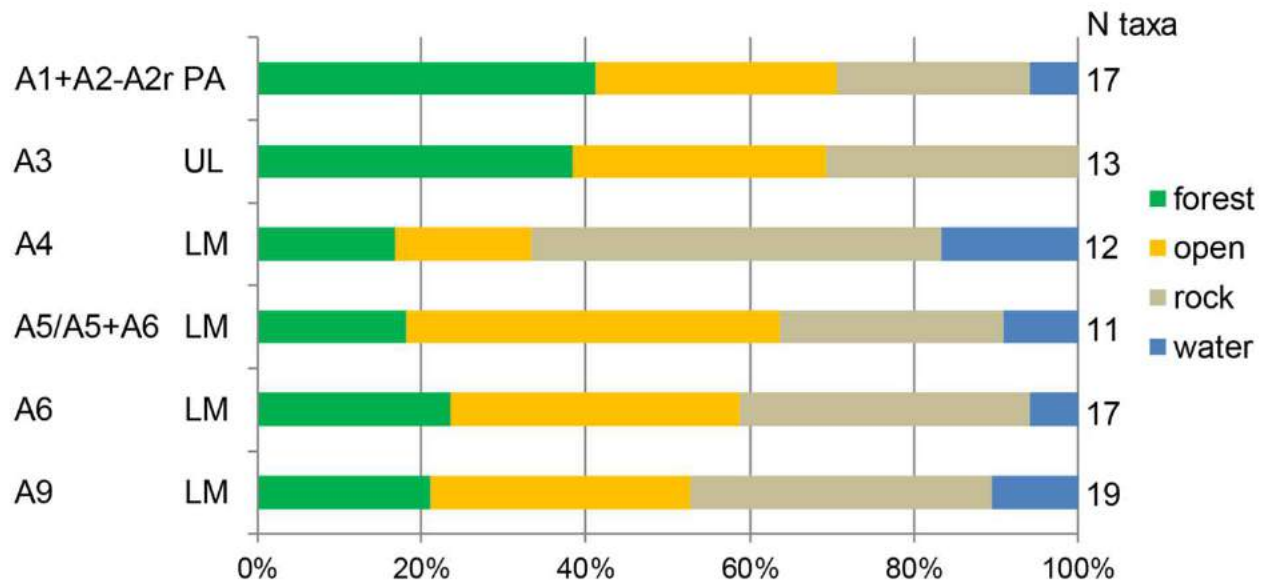


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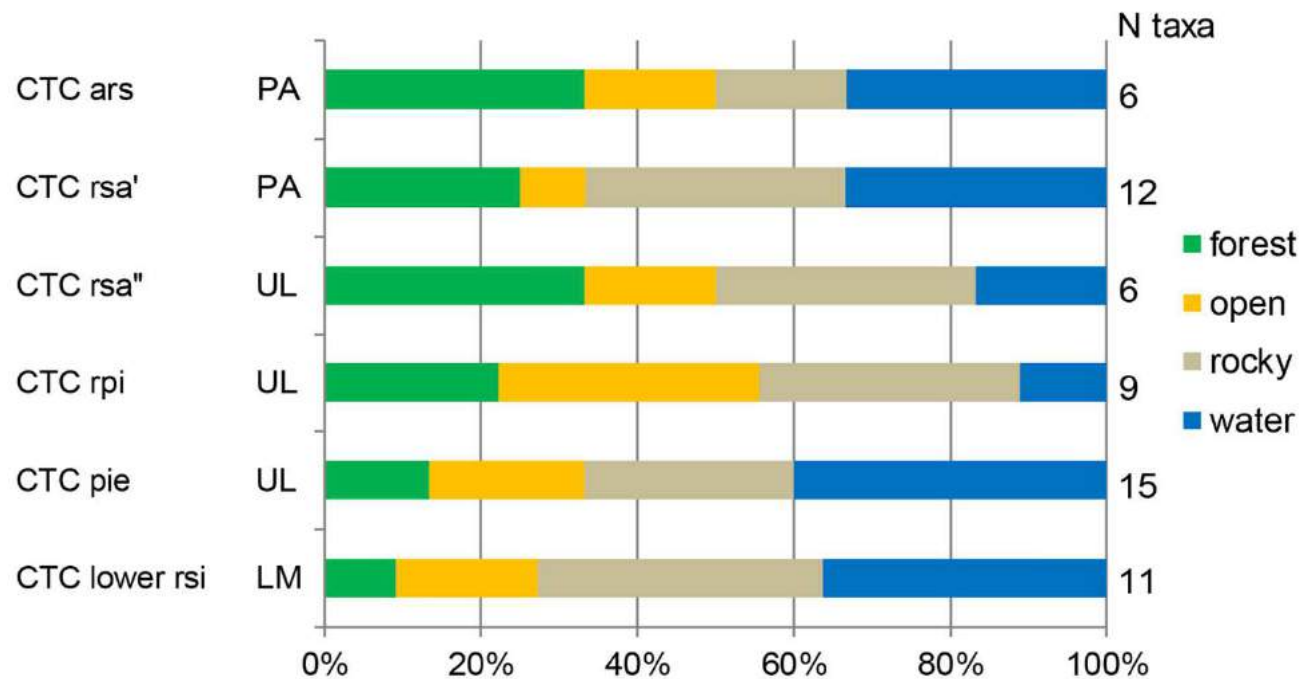


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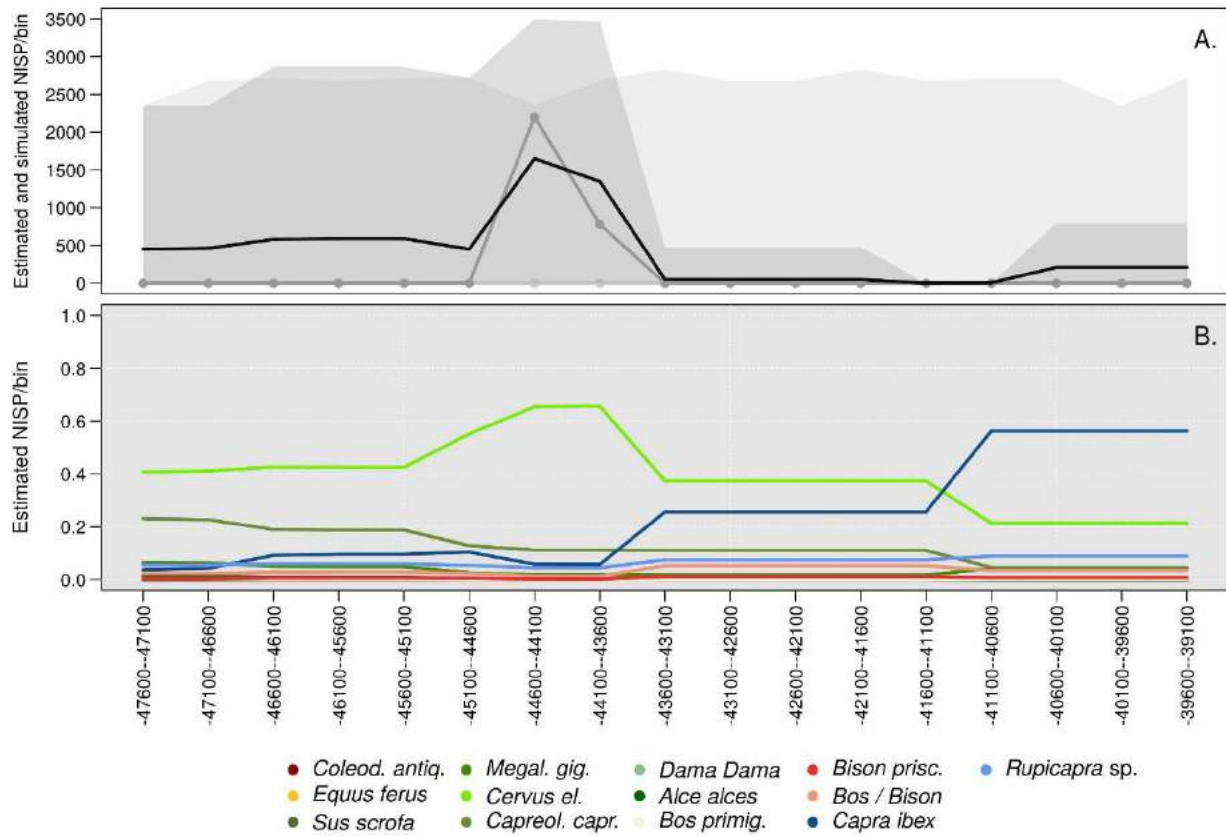


Figure 9

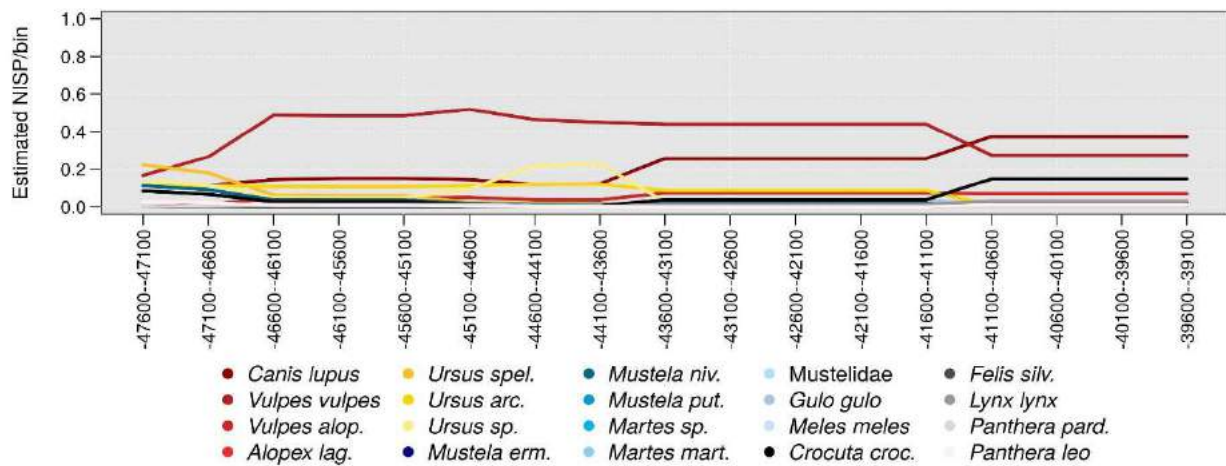
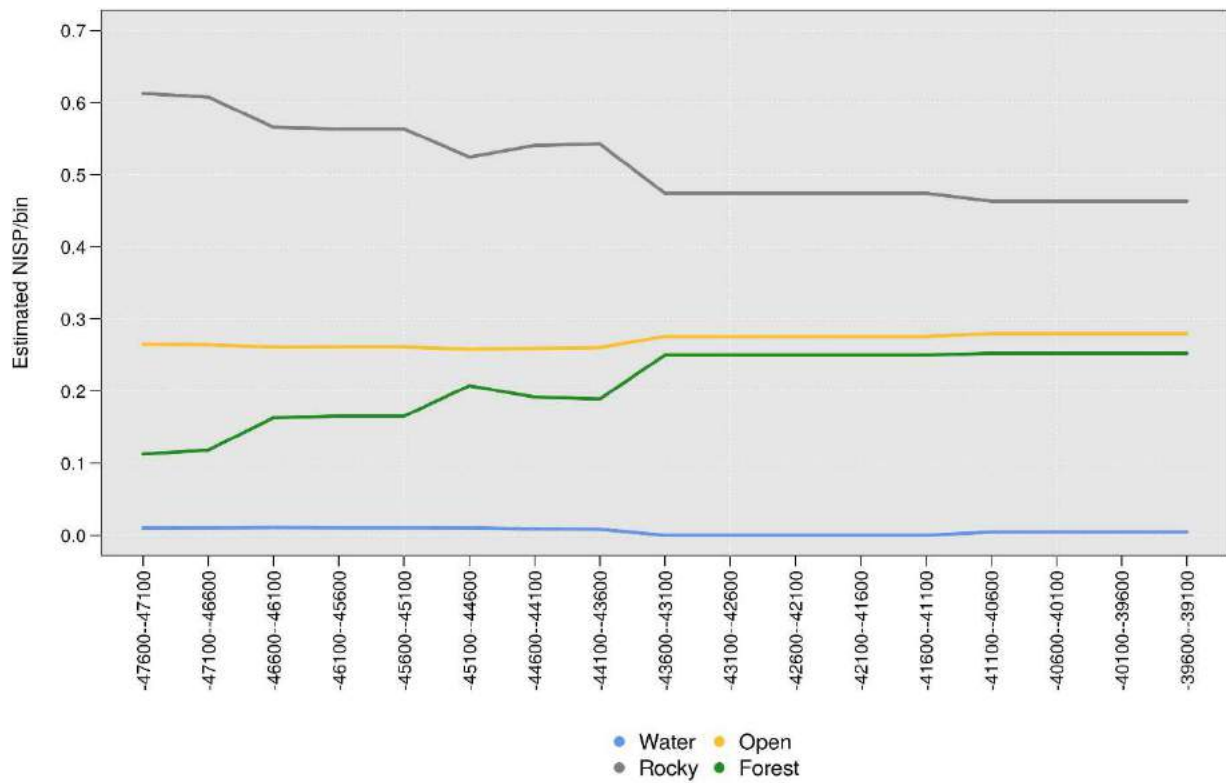


Figure 10





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1290 *Figure 11*



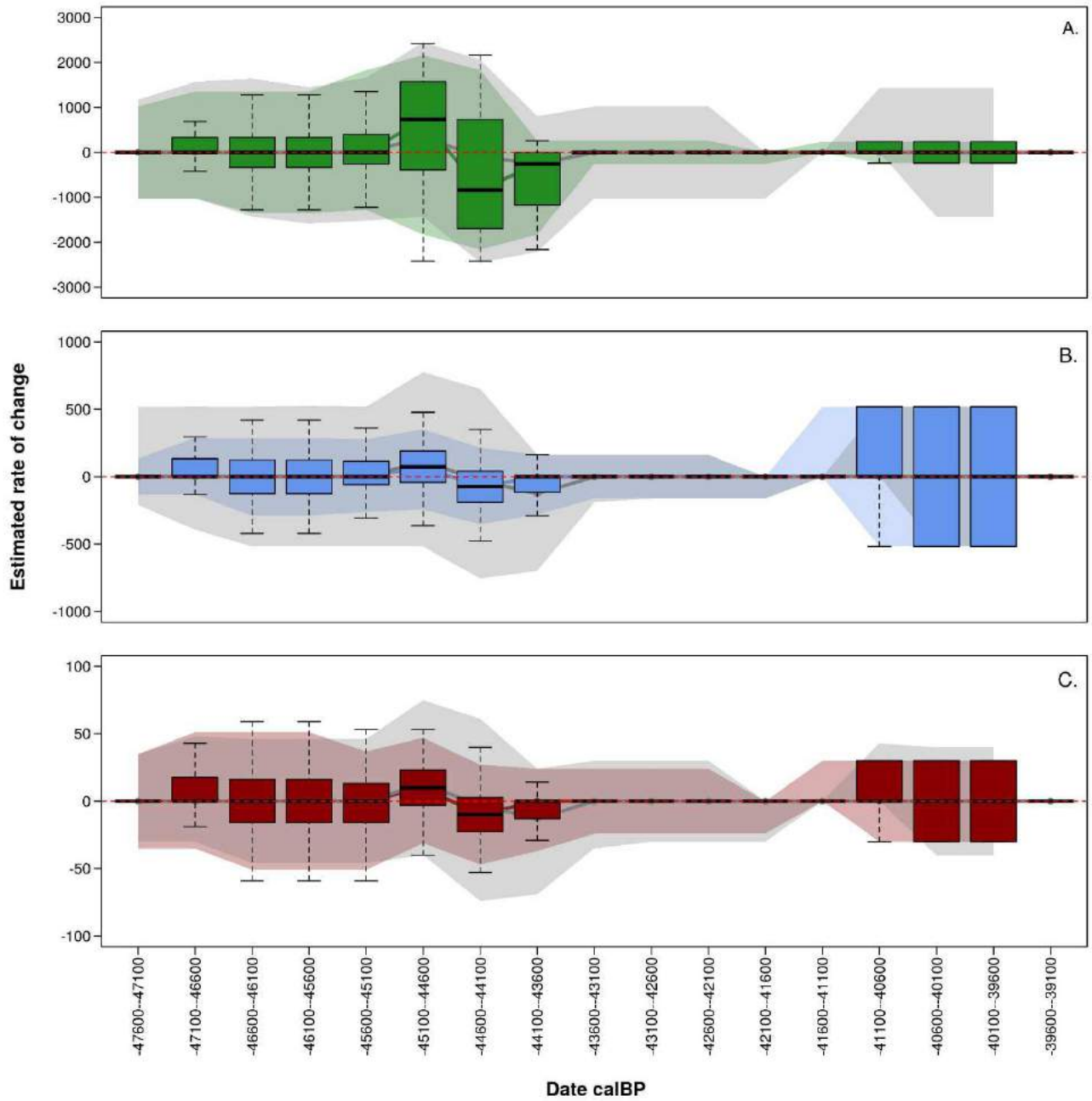
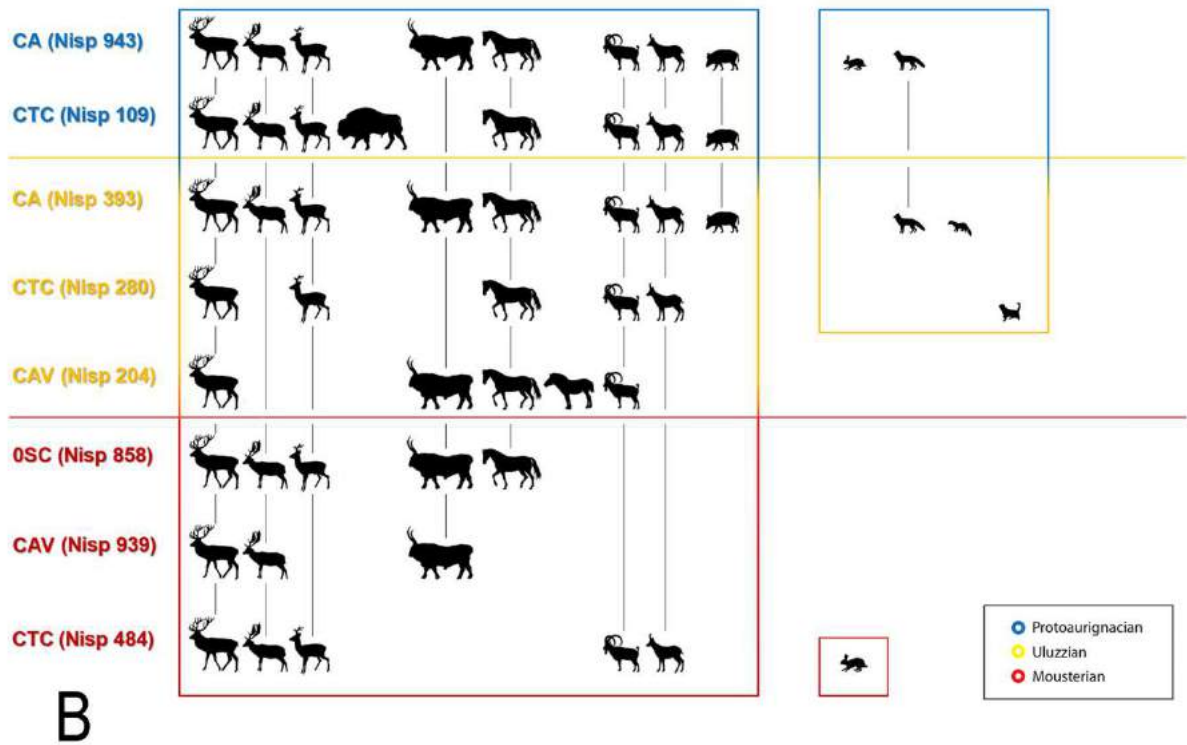
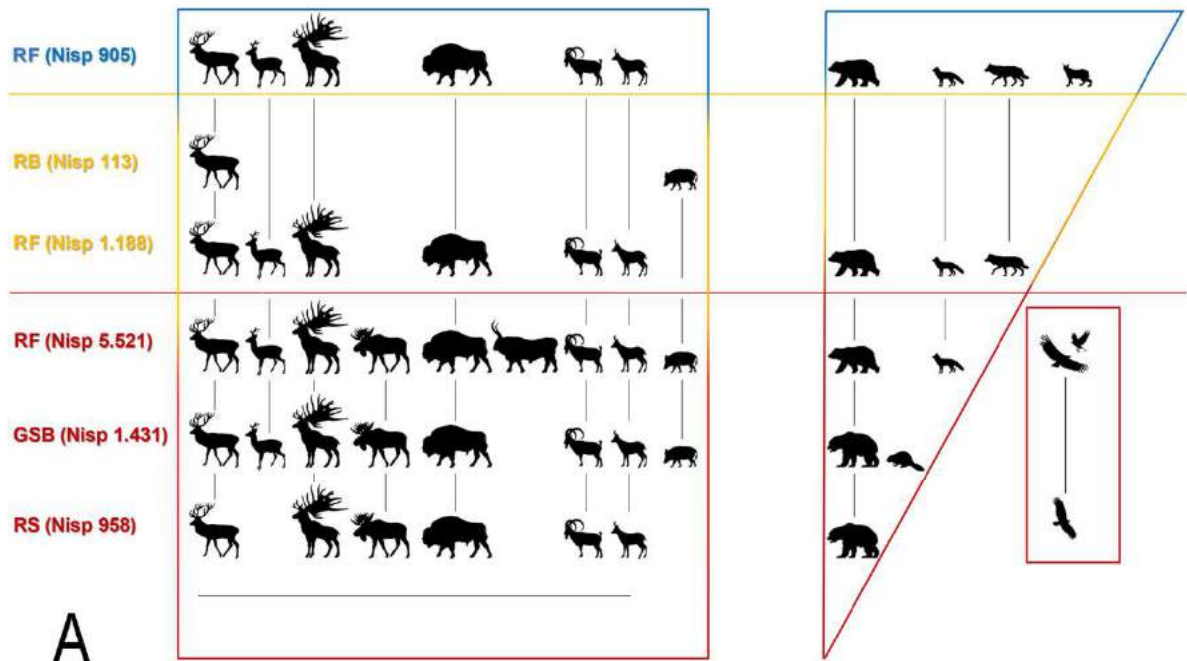


Figure 12

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1299 *Figure 13*

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1304 Table 1: separate excel file

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US - Levels	Technocomplex	0.1 - 1 cm	%	1 - 3 cm	%	Δ 3 cm	%	TOTAL Rem.	Burn.+Calc.	%	Burned	%	Calcined	%
RF A2-A2R	PA	13042	65.8	6280	31.7	507	2.6	19829	7861	40				
RF A3	UL	7831	46.1	8231	48.4	927	5.5	16989	4723	28	2840	60.1	1883	39.9
RB 1e+1f+1g	UL	33199	88.8	3748	10	443	1.2	37390	18464	49	15595	84.5	2869	15.5
RF A4	LM	9770	49	9287	46.5	898	4.5	19955	7321	37	5187	70.9	2134	29.1
SB II+III	LM	2744	29.8	5337	57.9	1136	12.3	9217	5431	59	4747	87.4	684	12.6
RS 5top+7	LM	43	8.2	47	9	434	82.8	524	693	8	42	97.7	1	2.3
RF A5/A5+A6	LM	35342	52.7	29767	44.4	1974	2.9	67083	38255	57	30442	79.6	7813	20.4
RF A6	LM	62692	56.5	43944	39.6	4408	4	111044	53413	48	46854	87.7	6559	12.3
RF A9	LM	78119	69.8	30763	27.5	2959	2.6	111841	54411	49	50398	92.6	4013	7.4
RS 5+8	LM	2307	53.6	1538	35.8	456	10.6	4301	43	16	671	96.8	22	3.2

1310

1311 Table 2

MODIF.	RS 5+8 LM		RF A9 LM		RF A6 LM		RF A5 LM		RS 5stop+7 LM		SB II+III LM		RF A4 LM		RB 1e+1f+1g UL		RF A3 UL		RF A2 PA	
	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%
CM+SCR	61	63.5	882	53.5	1003	37.8	399	35.5	76	67.3	92	54.8	626	68.9	16	59.3	289	53.4	348	64.7
CM+IF - CM+PM	10	10.4	143	8.7	171	6.5	50	4.4	20	17.7	14	8.3	128	14.1			106	19.6	30	5.6
IF+PM	25	26	623	37.8	1477	55.7	676	60.1	17	15	62	36.9	154	17	11	40.7	146	27	160	29.7
TOTAL BM	96		1648		2651		1125		113		168		908		27		541		538	

Table 3

1325

TECHNOCOMPLEX	LM		LM		LM		LM		LM		LM		LM		LM		LM		LM		LM		LM		UL		UL		UL		PA	
SITE - US/Lev.	RS 5+8		RF A9		RF A9		RF A6		RF A6		RF A5		RF A5		RS 5top+7		SB II+III		SB II+III		RF A4		RF A4		RB 1f+1g		RF A3		RF A3		RF A2	
Taxa	Ursus sp.		C. elaphus		C. capreolus		C. elaphus		C. capreolus		C. elaphus		C. capreolus		Ursus sp.		C. elaphus		C. capreolus		C. elaphus		Capra ibex		Sus scrofa		C. elaphus		Capra ibex		Capra ibex	
	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
Cranium	14	6.4	23	4.6	7	2.5	43	3.8	6	3.3	10	3.2	1	2	18	8.3	15	11.3	18	7.5	10	4.6	7	9.5	1	4.2	7	3.8	15	12.9	6	4.6
Emimandible	21	9.6	35	7.1	16	5.7	64	5.6	6	3.3	19	6.1	7	14	13	6	32	24.1	36	15.1	14	6.4	15	20.3	1	4.2	10	5.5	22	19	13	10
Tooth indet.	14	6.4	14	2.8	6	2.1	17	1.5	1	0.5	1	0.3			2	0.9			8	3.3	13	6	3	4.1	3	12.5	24	13.2	3	2.6	7	5.4
Hioyd	6	2.8					1				2	0.6			2	0.9	1	0.8									2	1.1			1	0.8
Atlas-axis	2	0.9					1	0.1							3	1.4																
Vertebra	21	9.6	3	0.6	2	0.7	7	0.6	1	0.5	2	0.6			12	5.6					2	0.9					2	1.1	1	0.9	3	2.3
Rib	39	17.9	4	0.8	2	0.7	7	0.6			1	0.3			54	25	1	0.8			1	0.5										
Clavicle															1	0.5																
Baculum	1	1.6													2	0.9																
Scapula	3	6.1					4	0.4	1	0.5					3	1.4							1	1.4			3	1.6		0	2	1.5
Humerus	2	0.9	27	5.5	12	4.3	89	7.8	5	2.7	24	7.7	1	6.25	3	1.4	5	3.8	2	0.8	6	2.8	4	5.4			9	4.9	4	3.4	6	4.6
Radius/Ulna							3				1	0.3					3	2.3					2	2.7					1	0.9		
Radius	3	1.4	29	5.9	10	3.6	69	6.1	6	3.3	14	4.5	1	2	15	6.9	3	2.3	2	0.8	10	4.6	2	2.7	1	4.2	5	2.7	3	2.6	6	4.6
Ulna	6	2.8	4	0.8	1	0.4	26	2.3	3	1.6	3	1			4	1.9	4	3	2	0.8	6	2.8					2	1.1	1	0.9	2	1.5
Carpals	6	2.8			6	2.1	8	0.7	5	2.7	1	0.3			7	3.2	1	0.8	1	0.4	1	0.5	4	5.4			1	0.5	9	7.8	3	2.3
Metacarpal	4	1.8	55	11.1	32	11.4	123	10.8	19	10.4	40	12.9	11	22	12	5.6	6	4.5	12	5	19	8.7	2	2.7	1	4.2	16	8.8	6	5.2	4	3.1
Metacarpal rud.					4	1.4	6	0.5	1	0.5			1	2					5	2.1											4	3.1

Coxal			4	0.8			5	0.4	2	1.1	1	0.3					1	0.8			1	0.5	2	2.7			2	1.1	3	2.6		
Femur	28	12.8	44	8.9	17	6	117	10.3	11	6	27	8.7	3	6	24	11.1	6	4.5	3	1.3	17	7.8	2	2.7			9	4.9	10	8.6	5	3.8
Patella	1	0.5			1	0.4					1	0.3	1	2					1	0.4												
Tibia	10	4.6	96	19.4	38	13.5	181	15.9	15	8.2	49	15.8			8	3.7	8	6	3	1.3	16	7.3	4	5.4			18	9.9	5	4.3	6	4.6
Fibula	4	1.8													4	1.9																
Malleolar bone							2	0.2	2	1.1											2	0.9	1	1.4							1	0.8
Calcaneum			1	0.2						1	0.5				2	0.9			1	0.4	1	0.5									1	0.8
Astragalus							1	0.1	2	1.1					1	0.5	1	0.8	1	0.4							1	0.5			3	2.3
Tarsals	1	0.5	2	0.4	1	0.4	3	0.3	2	1.1	2	0.6			3	1.4	2	1.5	1	0.4			2	2.7					1	0.9	4	3.1
Metatarsal	5	2.3	76	15.4	59	21	131	11.5	29	15.9	54	17.4	8	16	1	0.5	12	9	28	11.7	41	18.8	2	2.7	3	12.5	29	15.9	4	3.4	3	2.3
Metapodial	2	0.9	25	5.1	11	3.9	45	3.9	6	3.3	13	4.2	1	2			2	1.5	9	3.8	9	4.1			3		10	5.5	4	3.4	2	1.5
First phal.	11	5	11	2.2	21	7.5	28	2.5	7	3.8	10	3.2	1	2	8	3.7	8	6	35	14.6	7	3.2	8	10.8	3	12.5	4	2.2	4	3.4	12	9.2
Second phal.	6	2.8	12	2.4	9	3.2	50	4.4	15	8.2	16	5.1	6	12	8	3.7	9	6.8	24	10	15	6.9	3	4.1	3	12.5	10	5.5	3	2.6	9	6.9
Third phal.	6	2.8	4	0.8	4	1.4	28	2.5	1	0.5	6	1.9	2	4	6	2.8	3	2.3	13	5.4	4	1.8	1	1.4	1	4.2	5	2.7	2	1.7	6	4.6
First phal. rud.			3	0.6	4	1.4	9	0.8	4	2.2							1	0.8	4	1.7	2	0.9			3	12.5	2	1.1				
Sec. phal. rud.			5	1	4	1.4	14	1.2	7	3.8	3	1	2	4					7	2.9	8	3.7					4	2.2				
Th. phal. rud.			4	0.8	7	2.5	9	0.8	3	1.6	3	1					3	2.3	4	1.7	2	0.9					3	1.6				
Sesamoid	2	0.9	14	2.8	7	2.5	49	4.3	21	11.5	8	2.6	4	8			6	4.5	19	7.9	11	5	9	12.2	1	4.2	4	2.2	15	12.9	21	16.2
TOTAL	218		495		281		1140		182		311		50		216		133		239		218		74		24		182		116		130	
Tot Cranium + tooth	55	25.2	72	14.5	29	10.3	125	11	13	7.1	32	10.3	8	16	35	16.2	48	36.1	62	25.9	37	17	25	33.8	5	20.8	43	23.6	40	34.5	27	20.8
Tot trunk	63	28.9	7	1.4	4	1.4	15	1.3	1	0.5	3	1			72	33.3	1	0.8			3	1.4					2	1.1	1	0.9	3	2.3
Tot long limb bones	68	35.9	360	72.9	185	65.8	799	70.1	98	56.6	227	73	27	58.3	74	35.6	50	38.3	67	28.9	125	58.7	21	29.7	8	20.8	103	57.1	41	35.3	40	34.6
Carpal + tarsal	7	3.2	3	0.4	7	2.5	14	1	12	3.8	3	1			13	4.6	4	2.3	4	0.8	4	0.5	7	8.1			2	0.5	10	8.6	12	5.4
Phalan + sesamoides	25	11.5	53	10.7	56	19.9	187	16.4	58	31.9	46	14.8	15	30	22	10.2	30	22.6	106	44.4	49	22.5	21	28.4	11	45.8	32	17.6	24	20.7	48	36.9

1326

1327 Table 4

SITE	Technocomplex	1 - 3 cm	%	> 3 cm	%	TOTAL Rem.	Burn.+Calc.	%
US - Levels								
CAV EIII	UL	4201	79.9	984	20.1	5185	3452	82.2
CTC LM	LM	1764	91.9	156	8.1	1920	Not avail.	Not avail.
CAV FII	LM	9836	87.7	1378	12.3	11214	1744	17.7
OSC US 4/1	LM	17472	97.4	449	2.6	17921	12137	67.7

Table 5

MODIF.	CTC LM		CAV FII LM		OSC US 4 LM		CAV EII5 UL		CTC UL		CTC PA	
	NR	%	NR	%	NR	%	NR	%	NR	%	NR	%
CM+SCR	9	0.4	63	67	1	3.3	75	80.6	16	89	5	17.2
CM+IF / CM+PM	43	45.3	13	13.8	26	83.9	11	11.8	1	5.5	12	41.4
IF+PM	43	45.3	18	19.2	4	2.8	7	0.6	1	5.5	12	41.4
TOTAL BM	95		94		31		93		18		29	

Table 6

1344

TECHNOCOMPLEX	LM		LM		LM		UL		UL		UL		PA		PA	
SITE - US/Lev.	OSC		CTC		CAV(all lev.)		CAV EIII5		CTC		CALA 14		CTC ars-gic		CALA 13-10	
TAXA	<i>Bos primig.</i>		<i>Dama dama</i>		<i>Bos primig.</i>		<i>Bos primig.</i>		<i>C. elaphus</i>		<i>Dama dama</i>		<i>C. elaphus</i>		<i>C. elaphus</i>	
	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
Antler/Horn									3	3.2					1	0.2
Cranium	13	2.6	4	2.8	3	0.8	2	2.3	1	1	5	3.4			17	3.5
Emimandible	43	8.7	9	6.3	12	3			4	4.4	13	8.7	1	4.3	42	8.8
Deciduous teeth	8	1.6	9	6.3	49	12.4	1	1.2	2	2.1			2	8.7		
Permanent teeth	202	40.6	60	41.7	201	51	10	11.6	7	7.5			8	34.8		
Perm.+Deciduous teeth	11	2.2									46	30.9			133	27.8
Tooth indet.	47	9.5	10	6.9	21	5.3	5	5.8			2	1.3	2	8.7	7	1.5
Hioyd					7	1.8	1	1.2								
Atlas-axis																
Vertebra									3	3.3	1	0.7			2	0.4
Rib									1	1						
Clavicle																
Scapula															1	0.2
Humerus	10	2	3	2.1			4	4.7	5	5.5	2	1.3			9	1.9
Radius/Ulna	5	1					2	2.3	1	1						
Radius	10	2	5	3.5	9	2.3	1	1.2	4	4.4	6	4			12	2.5
Ulna	4	0.8			4	1	1	1.2			1	0.7			6	1.3



Carpals			2	1.4			4	4.7	8	8.7	3	2			15	3.1	
Metacarpal	12	2.4	3	2.1	8	2	2	2.3	16	17.2				3	13	38	7.9
Metacarpal rud.																	
Coxal																1	0.2
Femur	5	1	4	2.8					4	4.4						2	0.4
Patella									1	1	1	0.7				1	0.2
Tibia	51	10.3			3	0.8	3	3.5	9	9.7	4	2.7				5	1
Fibula																	
Malleolar bone							1	1.2								3	0.6
Calcaneum																	
Astragalus																	
Tarsals	7	1.4	2	1.4	6	1.5	6	7			14	9.4				14	2.9
Metatarsal	38	7.6	12	8.3	21	5.3	5	5.8	14	15	22	14.7	3	13.2		78	16.3
Metapodial	4	0.8	3	2.1	16	4.1	2	2.3			8	5.4	2	8.7		24	5
First phal.	13	2.6	6	4.2	15	3.8	16	18.6	7	7.5	12	8.1	1	4.3		29	6.1
Second phal.	6	1.2	9	6.3	4	1	8	9.3	2	2.1	6	4	1	4.3		21	4.4
Third phal.	1	0.2	2	1.4	1	0.3	1	1.2								9	1.9
First phal. rud.																	
Sec. phal. rud.																	
Th. phal. rud.																	
Sesamoid	7	1.5	1	0.4	14	3.6	11	12.6	1	1	3	2				9	1.9
TOTAL	497		144		394		86		93		149		23			479	
Tot Cranium + tooth	324	65.2	92	63.8	293	74.4	19	22.1	17	18.3	66	44.3	13	56.5		200	41.7
Tot trunk									4	4.3	1	0.7				4	0.9
Tot long limb bones	146	29.4	30	20.8	61	15.5	21	24.4	53	57	44	29.5	8	34.8		178	37.2
Carpal + tarsal			5	3.6	6	1.5	10	11.6	8	8.6	17	11.4				29	6
Phal. + sesamoides	27	5.4	17	11.8	34	8.6	36	41.9	11	11.8	21	14.1	2	8.7		68	14.2

Table 7

1347

1348 Appendices

Journal Pre-proof

	RS 5+8 - LM		RF A9 - LM		RF A6 - LM		RF A5/A5+A6 - LM		RS 5top+7 - LM		SB II+III - LM		RF A4 - LM		RB 1f-1g - UL		RF A3 - UL		RF A2-A2R - PA	
Taxa	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
<i>Stephanorhinus</i> sp.											2	0.3								
<i>Coelodonta antiquitatis</i>																	1	0.2		
<i>Sus scrofa</i>	2	4.8	2	0.2	2	0.1			1	1.7	36	5.2			21	35.6				
<i>Megaloceros giganteus</i>	5	11.9	79	6.5	28	1.8	10	2.1	14	24.1	12	1.7	12	2.5	2	3.4	8	1.8	34	4.3
<i>Cervus elaphus</i>	7	16.7	495	40.8	1095	69.7	297	62	6	10.3	136	19.6	242	50	5	8.5	169	37.4	170	21.4
<i>Capreolus capreolus</i>	1	2.4	281	23.1	182	11.6	48	10			251	36.2	54	11.2	3	5.1	50	11.1	37	4.7
<i>Alces alces</i>	2	4.8	17	1.4	4	0.3	1	0.2	5	8.6	24	3.5			3	5.1				
Cervidae	6	14.3	166	13.7	128	8.2	39	8.1	19	32.8	135	19.5	29	6	13	22	33	7.3		
<i>Bos primigenius</i>			6	0.5							1	0.1			1	1.7			2	0.3
<i>Bison priscus</i>	1	2.4	6	0.5	2	0.1			2	3.4			5	1	1	1.7	5	1.1	6	0.8
<i>Bos/Bison</i>	10	23.8	29	2.4	13	0.8	10	2.1	8	13.8	33	4.8	16	3.3	1	1.7	24	5.3	28	3.5
<i>Capra ibex</i>	5	11.9	46	3.8	54	3.4	30	6.3	2	3.4	3	0.4	82	16.9	1	1.7	116	25.7	447	56.2
<i>Rupicapra rupicapra</i>	3	7.1	68	5.6	55	3.5	32	6.7			53	7.6	31	6.4	4	6.8	34	7.5	71	8.9
Caprinae			19	1.6	7	0.4	12	2.5	1	1.7	8	1.2	13	2.7	4	6.8	12	2.7		
Total Ungulata	42		1214		1570		479		58		694		484		59		452		795	

Table A.1

	RS 5+8 - LM		RF A9 - LM		RF A6 - LM		RF A5/A5+A6 - LM		RS 5top+7 - LM		SB II+III - LM		RF A4 - LM		RB 1e+1f+1g - UL		RF A3 - UL		RF A2-A2R - PA	
Taxa	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
<i>Canis lupus</i>	3	1.3	4	11.1	7	11.9	4	7.7			3	1.8	11	11.5			21	25.6	38	37.3
<i>Vulpes vulpes</i>	3	1.3	6	16.7	20	33.9	26	50	1	0.5	9	5.5	61	63.5	4	9.5	36	43.9	28	27.5
<i>Vulpes/alopex</i>							3	5.8					5	5.2			6	7.3	7	6.9
<i>Alopex lagopus</i>																			2	2
<i>Ursus spelaeus</i>	157	66.2	8	22.2			2	3.8	148	66.7	100	61.3	2	2.1	21	50			1	1
<i>Ursus arctos</i>	1	0.4	4	11.1	10	16.9	4	7.7	6	2.7	3	1.8	11	11.5			7	8.5	1	1
<i>Ursus sp.</i>	64	27	5	13.9	21	35.6	13	25	66	29.7	38	23.3	2	2.1	13	31	2	2.4	1	1
<i>Mustela erminea</i>	4	1.7															1	1.2	2	2
<i>Mustela nivalis</i>			4	11.1	1	1.7							1	1			2	2.4	1	1
<i>Mustela putorius</i>											2	1.2							1	1
<i>Martes martes</i>	3	1.3							1	0.5					1	2.4				
<i>Mustelidae</i>			1	2.																
<i>Gulo gulo</i>													1	1			3	3.7	1	1
<i>Meles meles</i>	2	0.8																		
<i>Crocota crocuta spelaea</i>			3	8.3													3	3.7	15	14.7
<i>Felis silvestris</i>											2	1.2			2	4.8				
<i>Lynx lynx</i>											4	2.5					1	1.2	3	2.9
<i>Panthera pardus</i>											1	0.6	2	2.1						
<i>Panthera leo spelaea</i>			1	2.8															1	1
<i>Felidae</i>											1	0.6			1	2.4				
Total Carnivora	237		36		59		52		222		163		96		42		82		102	

Table A.2

	RS 5+8 - LM	RF A9 - LM	RF A6 - LM	RF A5/A5+A6 - LM	RS 5top+7 - LM	SB II+III - LM	RF A4 - LM	RB 1e+1f+1g - UL	RF A3 - UL	RF A2-A2R - PA
<i>Taxa</i>	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp
<i>Marmota marmota</i>		8	1			18		3	2	2
<i>Lepus cfr. timidus</i>								2		4
<i>Lepus sp.</i>	1			1		3			3	1
<i>Castor fiber</i>						27		1		1
Total Lagomorpha and Rodentia	1	8	1	1	0	48	0	6	5	8

Table A.3

	CTC spits 30-33 LM		CTC spits 25-29 LM		CTC spits 21-24 LM		CTC spit 20 LM		CTC 18lower-19 LM		CTC spit 18upper UL		CTC spit 17-13 UL		CTC spits 12-10 lower UL		CALA 14 UL		CTC spits 10 upper-8 PA		CTC spit 7 – top of seq.PA		CALA 13 PA		CALA 12 PA		CALA 11-10 PA	
Taxa	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
Stephanorhinus					1	2.4										1	0.3											
Equus ferus			1	0.5	1	2.4	1	2			1	5.9	7	6	65	59.1	18	5.2	10	30.3	1	1.7	5	2.2	10	2.3	4	1.8
Sus scrofa	2	1.5	4	2.1	1	2.4							4	3.4	4	3.6	46	13.3	7	21.2	4	6.7	10	4.3	52	12.1	28	12.3
Cervs elaphus	28	21.4	49	26.2	16	39	8	16	6	13.6	1	5.9	33	28.2	15	13.6	58	16.7	6	18.2	26	43.3	132	57.4	213	49.8	134	58.8
Capreolus	4	3.1	8	4.3	4	9.8	8	16	5	11.4	5	29.4	24	20.5	5	4.5	34	9.8	2	6.1	8	13.3	8	3.5	44	10.3	17	7.5
Dama dama	51	38.9	63	33.7	11	26.8	5	10	7	15.9	1	5.9	16	13.7	3	2.7	152	43.8	1	3	1	1.7	42	18.3	62	14.5	18	7.9
Cervidae indet.	6	4.6	3	1.6			8	16			1	5.9	3	2.6	1	0.9	13	3.7			3	5	10	4.3	22	5.1	9	3.9
Bos primigenus																	16	4.6					7	3	8	1.9	2	0.9
Bison priscus	2	1.5	7	3.7			1	2			1	5.9	3	2.6	5	4.5			6	18.2	1	1.7						
Bos/Bison							2	4	2	4.5	1	5.9	3	2.6	4	3.6												
Capra ibex	13	9.9	34	18.2	2	4.9	2	4	2	4.5	1	5.9	5	4.3	6	5.5	3	0.9	1	3	3	5	12	5.2	14	3.3	15	6.6
Rupicapra sp	25	19.1	18	9.6	5	12.2	15	30	22	50	5	29.4	19	16.2	1	0.9	4	1.2			13	21.7	4	1.7	2	0.5	1	0.4
Caprinae																	2	0.6							1	0.2		
Total Ungulata	131		187		41		50		44		17		117		110		347		33		60		230		428		228	

1369

1370 Table A.4

1371  
1372

	CTC gar LM	CTC lower rsi LM	CTC spit 18 upper UL	CTC spits 17 -13 UL	CTC spits 12 – 10 lower UL	CALA 14 UL	CTC PA	CALA 13 PA	CALA 12 PA	CALA 11 PA	CALA 10 PA
Taxa	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp
<i>Canis lupus</i>					1		2	2	1		
<i>Vulpes vulpes</i>				2	2	9		2	1		
<i>Ursus spelaeus</i>		1			1						
<i>Ursus arctos</i>				4		7			2	1	
<i>Mustela nivalis</i>	1			1	2						
<i>Martes sp.</i>						14			1		
<i>Mustelidae</i>				2							
<i>Meles meles</i>				2							
<i>Crocuta crocuta spelaea</i>	11			1	6		1				
<i>Felis silvestris</i>				2	3	5		2			
<i>Panthera pardus</i>	3	1		3	2	17		4	6	3	
<i>Panthera leo spel.</i>											
Carnivora indet.	6	5	1	7	1	3	2	1	1	1	
Total Carnivora	21	7	1	24	18	55	5	11	12	5	0

1373

1374 Table A.5

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CAV Filleb-e LM  
CAV FIIIb-c-d LM  
CAV FI-II-IIIa LM  
OSC 4-13 LM  
OSC 3 LM  
OSC 2-29-30-31 LM  
OSC 1 LM  
CAV EIII 5 UL

Taxa	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%	Nisp	%
<i>Stephanorhinus sp.</i>							1	0.2	7	12.3						
<i>Equus ferus</i>	40	11.5	40	14.9	50	19.8	17	3	16	28.1	48	25.9	2	5	53	27.3
<i>Equus hydruntinus</i>															1	0.5
<i>Equus sp.</i>															1	0.5
<i>Sus scrofa</i>	1	0.3	4	1.5	2	0.8	1	0.2							1	0.5
<i>Cervus elaphus</i>	72	20.6	54	20.1	69	27.3	51	8.9	15	26.3	27	14.6	11	27.5	52	26.8
<i>Capreolus capreolus</i>			6	2.2	3	1.2	11	1.9	2	3.5	8	4.3	1	2.5		
<i>Dama dama</i>	7	2	83	31	20	7.9	38	6.6	1	1.8	12	6.5	6	15		
<i>Cervidae indet.</i>	2	0.6	15	5.6	8	3.2	6	1			3	1.6				
<i>Bos primigenus</i>	227	65	66	24.6	101	39.9	445	77.5	15	26.3	82	44.3	20	50	86	44.3
<i>Capra ibex</i>							1	0.2	1	1.8	5	2.7				
<i>Rupicapra sp.</i>							3	0.5								
Total Nisp	349		268		253		574		57		185		40		194	

Table A.6



1413  
1414  
1415  
1416  
1417  
1418  
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1420  
1421  
1422

CAV FIII LM  
CAV F II LM  
OSC US 4-13 LM  
OSC US 3 LM  
OSC US 2-29-31 LM  
OSC US 1 LM  
CAV EIII5 UL

<i>Taxa</i>	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp	Nisp
<i>Canis lupus</i>			1				2
<i>Vulpes vulpes</i>	42	13					4
<i>Ursus spelaeus</i>							
<i>Ursus arctos</i>							
<i>Mustela nivalis</i>							
<i>Martes sp.</i>							
<i>Mustelidae</i>							
<i>Meles meles</i>							
<i>Crocuta crocuta spelaea</i>							1
<i>Felis silvestris</i>	2						
<i>Panthera pardus</i>							
<i>Panthera leo spelaea</i>					1		
Carnivora indet.	2						
Total Carnivora	46	13	1	0	1	0	7

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1424 Table A.7

	FUMANE										CASTELCIVITA																
	A9 – LM		A6 – LM		A5/A5+A6 – LM		A4 - LM		A3 - UL		A1-2 PA			rsi lower - LM		pie -UL		rpi - UL		rsa" - UL		rsa' - PA		gic – PA		ars – PA	
	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%		NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%	NISP	%
<i>Coturnix coturnix</i>	3	0.6	1	0.9	1	0.6			2	1.6				1	2.3	5	3.3	2	2.4					2	25		
<i>Alectoris graeca</i>	2	0.4					1	0.7						5	11.6	24	15.8	20	23.5	6	23.1	19	24.4	1	12.5	10	43.5
<i>Perdix perdix</i>	2	0.4					3	2.1	1	0.8	1	0.4		5	11.6	45	29.6	30	35.3	11	42.3	11	14.1	1	12.5	5	21.7
<i>Lagopus cf. lagopus</i>			1	0.9																							
<i>Lagopus muta</i>			1	0.9					1	0.8	3	1.2															
<i>T. urogallus/L. tetr. tetr.</i>	2	0.4																									
<i>Lyrurus tetr. x</i>	24	5.1	8	6.9	22	12.5	28	19.4	24	18.9	45	18.3															
<i>cf. Lyrurus tetr. x</i>			3	2.6	6	3.4	2	1.4	2	1.6																	
Galliformes unid.	1	0.2			3	1.7																					
<i>Aythya nyroca</i>																2	1.3			2	7.7						
<i>Spatula querquedula</i>														1	2.3	13	8.6										
<i>Mareca strepera</i>														5	11.6							1	1.3				
<i>Mareca penelope</i>														1	2.3												
<i>Anas platyrhynchos</i>							1	0.7								1	0.7										
<i>Anas crecca</i>																						2	2.6			1	4.3
<i>Anas cf. crecca</i>	1	0.2																									
<i>Columba livia/oenas</i>	2	0.4																									
<i>Columba oenas</i>											1	0.4		2	4.7	11	7.2	9	10.6	1	3.8	6	7.7			2	8.7
<i>Columba palumbus</i>			1	0.9																							
<i>Caprimulgus europaeus</i>																								1	12.5		
<i>Rallus aquaticus</i>	2	0.4			1	0.6	1	0.7			1	0.4															
<i>Crex crex</i>	70	14.7	16	13.8	24	13.6	24	16.7	25	19.7	53	21.5				4	2.6	2	2.4			2	2.6			1	4.3

1	0.7			1	0.4			1	1	1
6	4.2	1	0.8	10	4.1	1	2.3	6		
2	1.4	2	1.6							
2	1.4	2	1.6	2	0.8					
		1	0.8							

1425 Table A.8

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Table A.9 (separate excel file)

Sites levels - US	Single teeth		Carpal and tarsal bones		Phalanges + sesamoides		Total ungulates
	NR	%	NR	%	NR	%	Nisp
CALA PA	299	35.4	188	22.3	115	13.6	844
CTC PA	2	5.6	4	11.1	5	13.9	38
CALA UL	137	41.5	31	9.4	41	12.4	331
CAV EIII5 UL	46	23.5	30	15.3	59	30.1	196
CTC UL	38	15.1	13	5.2	38	15.1	233
OSC US 2 LM	128	69.2	3	1.6	5	2.7	185
CAV str. F LM	552	65.3	12	1.4	67	7.9	845
CTC LM	6	9	3	4.5	9	13.4	67

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Table A.10

Elements	OSC US 4/1 LM	CAV FII LM	CTC LM	CAV EIII5 UL
	%	%	%	%
Antler/Horn	0.4	0.3		3.5
Skull	4.3	4.8	4.9	2.5
Mandible	0.4	0.4	2	0.7
Teeth	18.4	14.9	3.6	7.9
Vertebrae		3	4.6	3.3
Ribs	3.5	11.2	15.7	13.4
Scapula		2.3		0.4
Sternum			0.7	0.7
Pelvis	0.4		0.3	0.2
Metapodials			0.8	
Diaphysis	45.3	41.3	41.4	18.6
Epiphysis	5.6	8.2	8,2	12,9
Spongy bones	21.8	11.6	12	31.9
Total remains	5747	9574	1920	5185

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Table A.11

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Sites	US/levels	GM	(D)igested	TOT.Car.M	TOT %	TOT. NR
RS-Rio Secco	5+8	53	2	55	1.3	4301
RF-Fumane	A9	100	1	101	0.09	111841
RF-Fumane	A6	24	16	40	0.03	111044
RF-Fumane	A5/A5+A6	20	9	29	0.04	67083
RS-Rio Secco	5top+7	31	-	31	5.9	524
SB-S. Bernardino	II+III	61	1	62	0.6	9217
RF-Fumane	A4	51	17	68	0.3	19955
RB-Broion	1e+1f+1g	3	1	4	0.01	37390
RF-Fumane	A3	53	36	89	0.5	16989
RF-Fumane	A2-A2R	17	9	26	0.1	19829

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1477 Table A.12

1478

	Mann-Whitney W	P-value
1-3cm LM – UL Northern Italy	7	1
>3cm LM – UL Northern Italy	4	0.5
Burn.+Calc LM – UL Northern Italy	5	0.86

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1480 Table A.13

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	X-squared	df	P-value	Effect size (Cohen's h)	Power
1-3cm CAV UL – CAV LM	128,7	1	<0.001	-0,19	1
1-3cm CAV UL – OSC LM	1875,8	1	<0.001	-0,55	1
>3cm CAV UL – CAV LM	128,7	1	<0.001	0,19	1
>3cm CAV UL – OSC LM	1875,8	1	<0.001	0,58	1
Burn+Calc CAV UL – CAV LM	4264,7	1	<0.001	1,1	1
Burn+Calc CAV UL – OSC LM	2,4161	1	0,12	-0,04	0,72

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1483 Table A.14

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	X-squared	df	P-value	Effect size (Cohen's h)	Power
Carpal+tarsal CAV UL – CAV LM	19,344	1	<0.001	0,45	0,965
Carpal+tarsal CAV UL – OSC LM	52,104	1	<0.001	0,69	0,999
Phalang.+Sesamoides CAV UL – CAV LM	59,942	1	<0.001	0,81	0,999
Phalang.+Sesamoides CAV UL – OSC LM	97,192	1	<0.001	0,93	1

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1488 Table A.15

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	X-squared	df	P-value	Effect size (Cohen's h)	Power
Carpal+tarsal CAV UL – CAV LM	79,232	1	<0.001	0,57	0,999
Carpal+tarsal CAV UL – OSC LM	20,831	1	<0.001	0,55	0,999
Phalanges+Sesamoides CAV UL – CAV LM	73,523	1	<0.001	0,59	0,999
Phalanges+Sesamoides CAV UL – OSC LM	51,12	1	<0.001	0,83	1

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1491 Table A.16

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	X-squared	df	P-value	Effect size (Cohen's h)	Power
Diaphysis CAV UL – CAV LM	780,01	1	<0.001	0,5	1
Diaphysis CAV UL – OSC LM	883,87	1	<0.001	0,58	1
Epiphysis CAV UL – CAV LM	83,663	1	<0.001	0,15	1
Epiphysis CAV UL – OSC LM	176,26	1	<0.001	0,25	1
Spongy bones CAV UL – CAV LM	910,5	1	<0.001	0,55	1
Spongy bones CAV UL – OSC LM	142,45	1	<0.001	0,23	1

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1494 Table A.17

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1502 Figure A.1 separate excel file

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1506 Figure A.2 separate excel file

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	Sites	US/levels	Technocomplex	C14 cal BP	U/Th	Tot. NISP Ungulates	Dominant taxa	Climate/Environment	
Northern Italy	RS-Rio Secco	5+8	Late Mousterian	>48-44 ky BP	-	42	<i>Ursus</i> sp.	cold-temperate climate with humid condition and open environments	
	RF-Fumane	A9	Late Mousterian	47-45 ky BP	-	1214			
	RF-Fumane	A6	Late Mousterian	44-42 ky BP	-	1570	<i>Cervus elaphus</i> + <i>Capreolus capreolus</i>	temperate climate with forests and clearings	
	RF-Fumane	A5/A5+A6	Late Mousterian		-	479			
	RS-Rio Secco	5top+7	Late Mousterian	>49-41 ky BP	-	58	<i>Ursus</i> sp.	cold-temperate climate with humid condition and open environments	
	SB-S. Bernardino	II+III	Late Mousterian		35-54 ky	694	<i>Cervus elaphus</i> + <i>Capreolus capreolus</i>	temperate climate with humid conditions and woodland covering	
	RF-Fumane	A4	Late Mousterian	45-44 ky BP	-	484	<i>Cervus elaphus</i> + <i>Capra ibex</i>	cold-temperate climate with alpine setting and open environments	
	RB-Broion	1e+1f+1g	Uluzzian	38 ky BP	-	59	<i>Sus scrofa</i>	cold-temperate climate with humid woodlands	
Southern Italy	RF-Fumane	A3	Uluzzian	44-42 ky BP	-	452	<i>Cervus elaphus</i> + <i>Capra ibex</i>	cold-temperate climate with alpine setting and open environments	
	RF-Fumane	A2-A2R	Protoaurignacian	40-34 ky BP	-	795	<i>Capra ibex</i>	cold climate with steppic environments	
	Cala	R	Late Mousterian	-	-	-	-	-	
	CTC-Castelcivita	32-21	Late Mousterian		-		<i>Dama dama</i> + <i>Cervus elaphus</i>	temperate woodland covering	
	CTC-Castelcivita	20-18lower	Late Mousterian	46-42 ky BP	-	453	<i>Rupicapra</i> sp. + <i>Cervus elaphus</i>	woodland covering and increasing in humidity	
	CTC-Castelcivita	18upper-13	Uluzzian	-	-	134	<i>Capreolus capreolus</i> + <i>Rupicapra</i> sp.	temperate climate with more dispersed woodlands	
	CTC-Castelcivita	12-10	Uluzzian	42-40.5 ky BP	-	110	<i>Equus ferus</i>	cold climate and increased presence of open environments	
	Cala	14	Uluzzian	-	-	347	<i>Dama dama</i>	temperate climate and mediterranean evergreen	
Istria	CTC-Castelcivita	10upper-8	Protoaurignacian	-	-	33	<i>Equus ferus</i> + <i>Sus scrofa</i>	cold climate with woodland covering and open environments	
	CTC-Castelcivita	7-top sequence	Protoaurignacian	-	-	60	<i>Cervus elaphus</i> + <i>Rupicapra</i> sp.	cold-temperate climate	
	Cala	13	Protoaurignacian	-	-	230			
	Cala	12	Protoaurignacian	-	-	428	<i>Cervus elaphus</i>	onset of cold climate with dispersal woodlands	
	Cala	11-10	Protoaurignacian	-	-	228			
	CAV-Cavallo	FIIIE	Late Mousterian	-	-	349	<i>Bos primigenius</i> + <i>Cervus elaphus</i>	open/forest steppe	
	CAV-Cavallo	FIIIB-D	Late Mousterian	-	-	268	<i>Dama dama</i> + <i>Bos primigenius</i>	temperate phase	
	CAV-Cavallo	FIIIA-FI	Late Mousterian	>45 ky BP	-	253	<i>Bos primigenius</i> + <i>Cervus elaphus</i>	semi-arid stage/forest steppe	
Adriatic	OSC-Oscuruscuto	4-13	Late Mousterian	-	-	574	<i>Bos primigenius</i>	wooded meadows and open spaces	
	OSC-Oscuruscuto	3	Late Mousterian	-	-	57	<i>Equus ferus</i> + <i>Bos primigenius</i>	semi-arid stage/forest steppe	
	OSC-Oscuruscuto	2-29-30-31	Late Mousterian	-	-	185	<i>Bos primigenius</i> + <i>Equus ferus</i>	semi-arid stage/forest steppe	
	OSC-Oscuruscuto	1	Late Mousterian	43-42 ky BP	-	40	<i>Bos primigenius</i> + <i>Cervus elaphus</i>	temperate phase	
	CAV-Cavallo	EIII	Uluzzian	45-43 ky BP	-	194	<i>Bos primigenius</i> + <i>Equus ferus</i>	cold climate with more dispersed woodlands	

 cold

 temperate

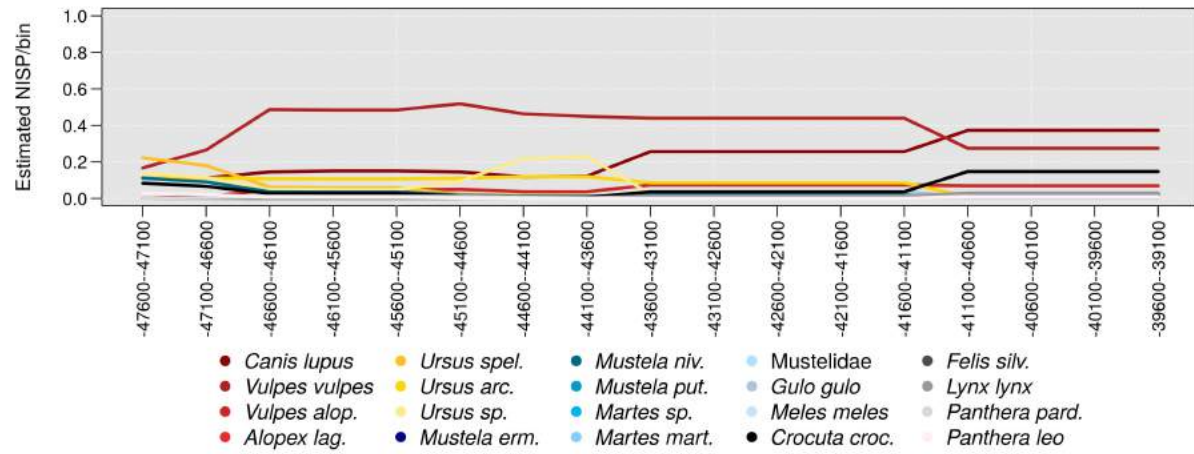
semi-arid  
cold/temperate

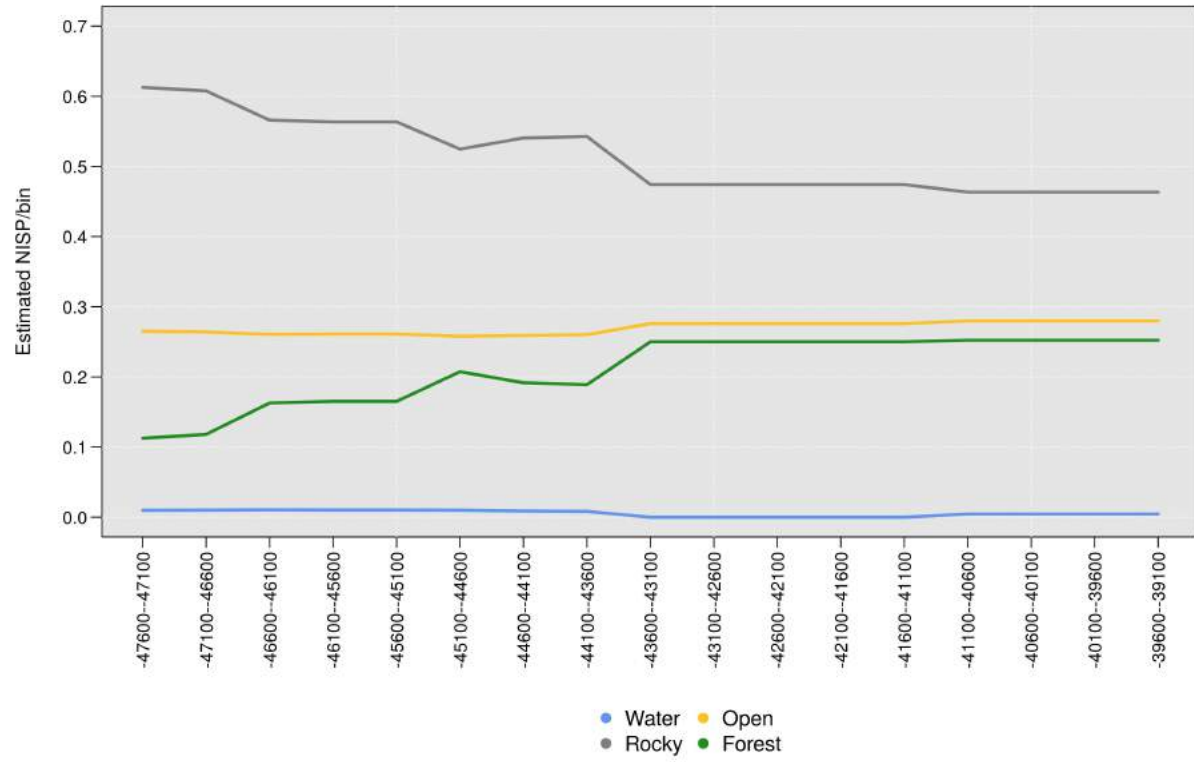
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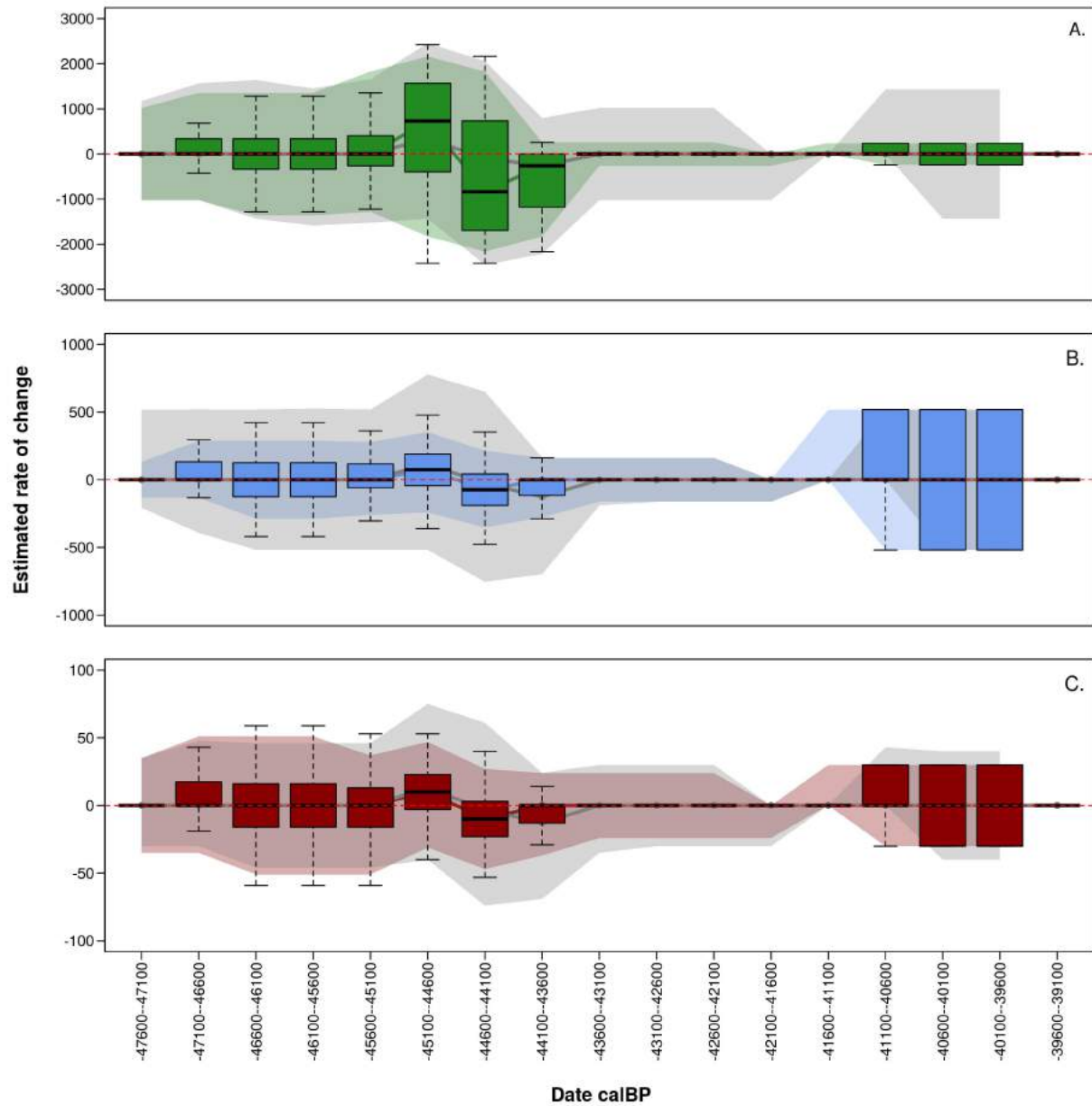
	site	Code(s)	Material	Method	Level	Detailed level	Technocomplex	14CAge	sd	Reference
1	Fumane	OxA-11347	Charcoal	ABA14C	A2	A2; sq. 97d	Protoaurignacian	30650	260	Higham et al 2009; Higham 2011
2	Fumane	OxA-17569	Charcoal	ABOX-SC_14C	A2	A2; sq. 97d	Protoaurignacian	35640	220	Higham et al 2009; Higham 2011
3	Fumane	OxA-11360	Charcoal	ABA14C	A2	A2; sq. 107i	Protoaurignacian	31830	260	Higham et al 2009; Higham 2011
4	Fumane	OxA-17570	Charcoal	ABOX-SC_14C	A2	A2; sq. 107i	Protoaurignacian	35180	220	Higham et al 2009; Higham 2011
5	Fumane	OxA-19411	Charcoal	ABA14C	A2	A2/ struc.17	Protoaurignacian	32530	240	Higham et al 2009; Higham 2011
6	Fumane	OxA-19413	Charcoal	ABA14C	A2	A2/struc.16/lev.B	Protoaurignacian	32120	240	Higham et al 2009; Higham 2011
7	Fumane	OxA-19414	Charcoal	ABOX-SC_14C	A2	A2/struc.16/lev.Ba	Protoaurignacian	34180	270	Higham et al 2009; Higham 2011
8	Fumane	OxA-19412	Charcoal	ABOX-SC_14C	A2	A2/struc.17a	Protoaurignacian	34940	280	Higham et al 2009; Higham 2011
9	Fumane	OxA-19525	Charcoal	ABA14C	A2	A2/struc.18	Protoaurignacian	33380	210	Higham et al 2009; Higham 2011
10	Fumane	OxA-19584	Charcoal	ABOX-SC_14C	A2	A2/struc.18	Protoaurignacian	35850	310	Higham et al 2009; Higham 2011
11	Fumane	Oxa-21736	Mammal Bone	14C-ultrafiltration	A3	A3	Uluzzian	39100	1000	Douka et al 2014
12	Fumane	Oxa-X-2295-52	Mammal Bone	14C-ultrafiltration	A3	A3	Uluzzian	41300	1300	Douka et al 2014
13	Fumane	Oxa-21735	Mammal Bone	14C-ultrafiltration	A4	A4/struct. II/744	Late Mousterian	42000	1700	Douka et al 2014
14	Fumane	Oxa-21733	Mammal Bone	14C-ultrafiltration	A4	A4II	Late Mousterian	41000	1300	Douka et al 2014
15	Fumane	Oxa-21734	Mammal Bone	14C-ultrafiltration	A4	A4II	Late Mousterian	42000	1400	Douka et al 2014
16	Fumane	OxA-17566	Charcoal	ABOX-SC_14C	A5	A5 + A6, sq.90	Late Mousterian	40460	360	Higham et al 2009; Higham 2011
17	Fumane	OxA-17567	Charcoal	ABA14C	A5	A5 + A6, sq.90	Late Mousterian	39500	330	Higham et al 2009; Higham 2011
18	Fumane	OxA-17568	Charcoal	ABA14C	A5	A5 + A6, sq.90	Late Mousterian	39490	350	Higham et al 2009; Higham 2011
19	Fumane	OxA-8022	Charcoal	ABA14C	A5	A5 + A6, sq.90	Late Mousterian	38800	750	Higham et al 2009; Higham 2011
20	Fumane	OxA-8023	Charcoal	ABA14C	A5	A5 + A6, sq.90	Late Mousterian	38250	700	Higham et al 2009; Higham 2011
21	Fumane	OxA-19410	Charcoal	ABA14C	A5	A5 sq. 88i,3789/stru	Late Mousterian	34500	270	Higham et al 2009; Higham 2011
22	Fumane	OxA-X-2275-45	Charcoal	ABOX-SC_14C	A5	A5 sq. 88i,3789/stru	Late Mousterian	41650	650	Higham et al 2009; Higham 2011
23	Fumane	OxA-17980	Charcoal	ABOX-SC_14C	A5	A5, sqs. 85,86,95,9	Late Mousterian	40150	350	Higham et al 2009; Higham 2011
24	Fumane	OxA-18199	Charcoal	ABA14C	A5	A5, sqs. 85,86,95,9	Late Mousterian	36860	700	Higham et al 2009; Higham 2011
25	Fumane	OxA-6463	Charcoal	ABA14C	A5	A5, sqs. 85,86,95,9	Late Mousterian	33700	600	Higham et al 2009; Higham 2011
26	Fumane	OxA-21796	Bone	14C-ultrafiltration	A2		Protoaurignacian	35400	750	Higham 2011
27	Fumane	OxA-21712	Bone	14C-ultrafiltration	A5		Late Mousterian	40000	1100	Higham 2011
28	Fumane	OxA-21809	Bone	14C-ultrafiltration	A5	A5+A6	Late Mousterian	40200	1200	Higham 2011
29	Fumane	OxA-21758	Bone	14C-ultrafiltration	A5	A5+A6	Late Mousterian	41100	1300	Higham 2011
30	Fumane	OxA-21757	Bone	14C-ultrafiltration	A5	A5+A6	Late Mousterian	41500	1500	Higham 2011
31	R. Broion	OxA-35527	Bone	14C	1g	1g	Uluzzian	38900	1000	Peresani et al. 2019
32	Rio Secco	S-EVA25353/MAMS15230	Bone with cutmarks	14C	5 top	I14 b	Mousterian	44100	660	Talamo et al., 2014
33	Rio Secco	S-EVA25355/MAMS15231	Bone with cutmarks	14C	5 top I	G14III	Mousterian	45695	790	Talamo et al., 2014
34	Rio Secco	S-EVA25356/MAMS15232	Bone	14C	5 top II	H14IV	Mousterian	43210	600	Talamo et al., 2014
35	Rio Secco	S-EVA25357/MAMS15233	Bone with cutmarks	14C	5 top I	I14II	Mousterian	45740	800	Talamo et al., 2014
36	Rio Secco	S-EVA25359/MAMS15235	Bone	14C	7	H14h	Mousterian	46320	1430	Talamo et al., 2014
37	Rio Secco	S-EVA25361/MAMS15236	Bone with cutmarks	14C	7	H13IV	Mousterian	>49000		Talamo et al., 2014
38	Rio Secco	S-EVA25362/MAMS15237	Bone with cutmarks	14C	7	H13IV	Mousterian	44560	1150	Talamo et al., 2014
39	Rio Secco	S-EVA25363/MAMS15238	Bone with cutmarks	14C	7	H14g	Mousterian	44770	1180	Talamo et al., 2014
40	Rio Secco	OxA-25359	Charcoal	14C	8	sq.H11IV n.17	Mousterian	42000	900	Peresani et al., 2014; Talamo et al., 2014
41	Rio Secco	LTL429A	Bone	14C	5 top II	GRSI	Mousterian	37790	360	Peresani et al., 2014; Talamo et al., 2014
42	S. Bernardino			U/Th ESR	II		Mousterian	52000	5000	
43	S. Bernardino			U/Th ESR	II		Mousterian	38000	5000	Gruppioni 2003; Lopez Garcia 2017; Peresani et al. 2015
44	S. Bernardino			U/Th ESR	II		Mousterian	35000	4000	Gruppioni 2003; Lopez Garcia 2017
45	S. Bernardino			U/Th ESR	II		Mousterian	49000	5000	
46	S. Bernardino			U/Th ESR	II		Mousterian	54000	5000	
47	Castelcivita	GrN-13984	Charcoal	14C	cgr	spits 29-30	Late Mousterian	42700	900	Gambassini 1997
48	Castelcivita	GrN-13982	Charcoal	14C	cgr	spits 29-30	Late Mousterian	39100	1300	Gambassini 1997
49	Castelcivita	Oxa-22622	Charcoal	ABOX-SC_14C	rsa"	spit 11	Uluzzian	36120	360	Wood et al. 2012
50	Oscurusciuto	Beta 181165	Mammal bone	14C		1	Late Mousterian	38500	900	Marciani et al. 2016
51	Oscurusciuto		Tephra	Ar <sup>40</sup> /Ar <sup>39</sup>		14 1-TM19	Mousterian	-55000		Spagnolo et al., 2016
57	Cavallo	Oxa-19254	Shell	14C	D1=D1b		Uluzzian	35080	230	Benazzi et a. 2011
58	Cavallo	Oxa-19255	Shell	14C	D2=D1b		Uluzzian	36260	250	Benazzi et a. 2011
59	Cavallo	Oxa-20631	Shell	14C	DII		Uluzzian	36780	310	Benazzi et a. 2011
60	Cavallo	Oxa-19257	Shell	14C	D3=DII		Uluzzian	42360	400	Benazzi et a. 2011
61	Cavallo	Oxa-19258	Shell	14C	D8=DII?	Page 1	Uluzzian	36000	400	Benazzi et a. 2011

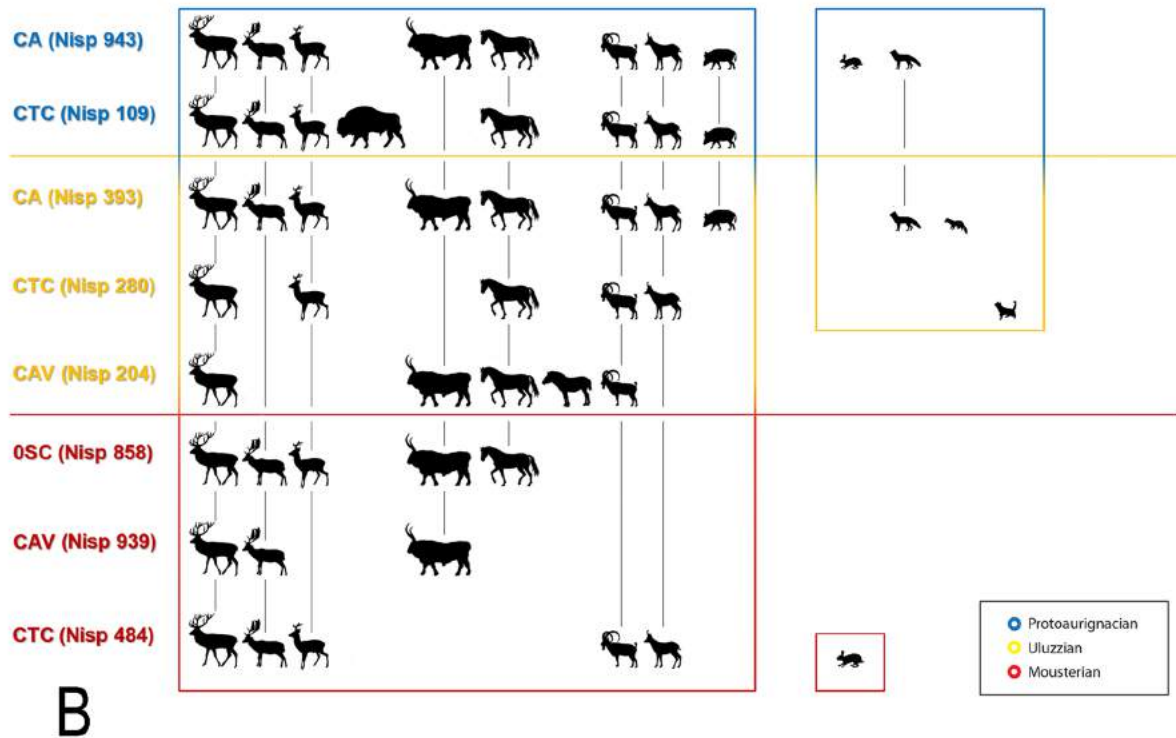
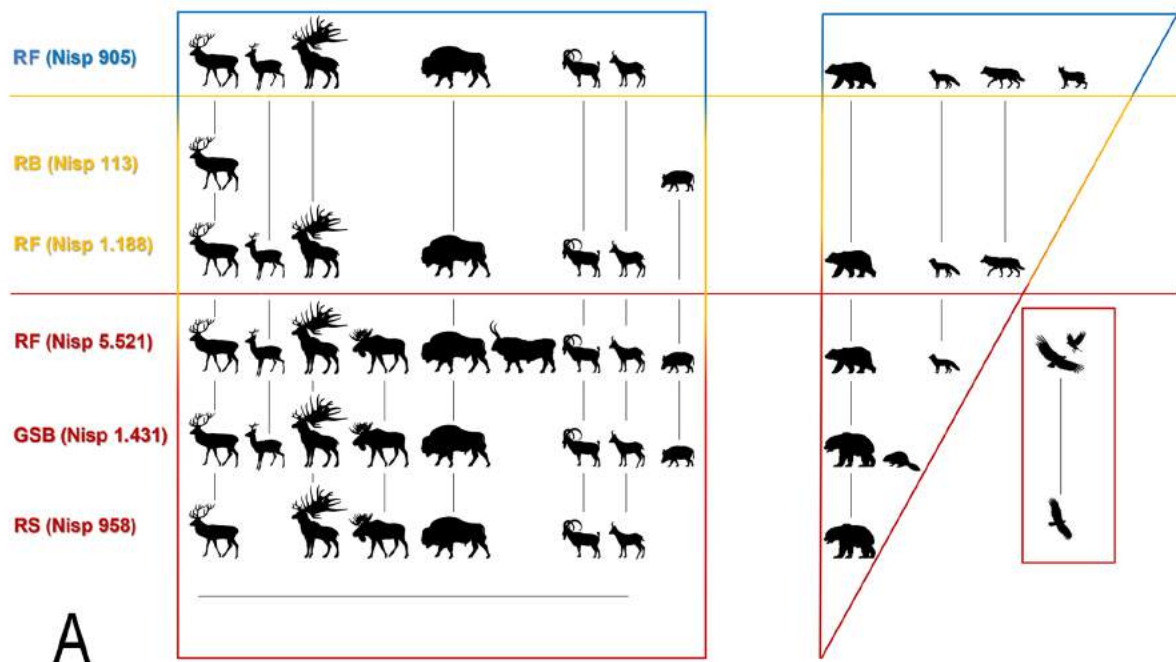
62	Cavallo	Oxa-19256	Shell	14C	E1=E-D	tableS2	Uluzzian	39060	310	Benazzi et al. 2011
63	Cavallo	Oxa-X2280-16	Shell	14C	E1=E-D		Uluzzian	38300	400	Benazzi et al. 2011
64	Cavallo	Oxa-19242	Shell	14C	E4=EII-I		Uluzzian	39990	340	Benazzi et al. 2011
65	Cavallo	Fi0822	Charcoal	ABA14C	FII		Mousterian	42000	2400	Fabbri et al. 2016
66	Cavallo	Fi0824	Charcoal	ABA14C	FII		Mousterian	39300	1900	Fabbri et al. 2016
67	Cavallo		Tephra	Ar <sup>40</sup> /Ar <sup>39</sup>	Fa-Y6			45500	1000	Zanchetta et al. 2018
68	Cavallo		Tephra	Ar <sup>40</sup> /Ar <sup>39</sup>	CII-Y5			39850	140	Zanchetta et al. 2018

Most recent available absolute datings for the sampled archaeological sites

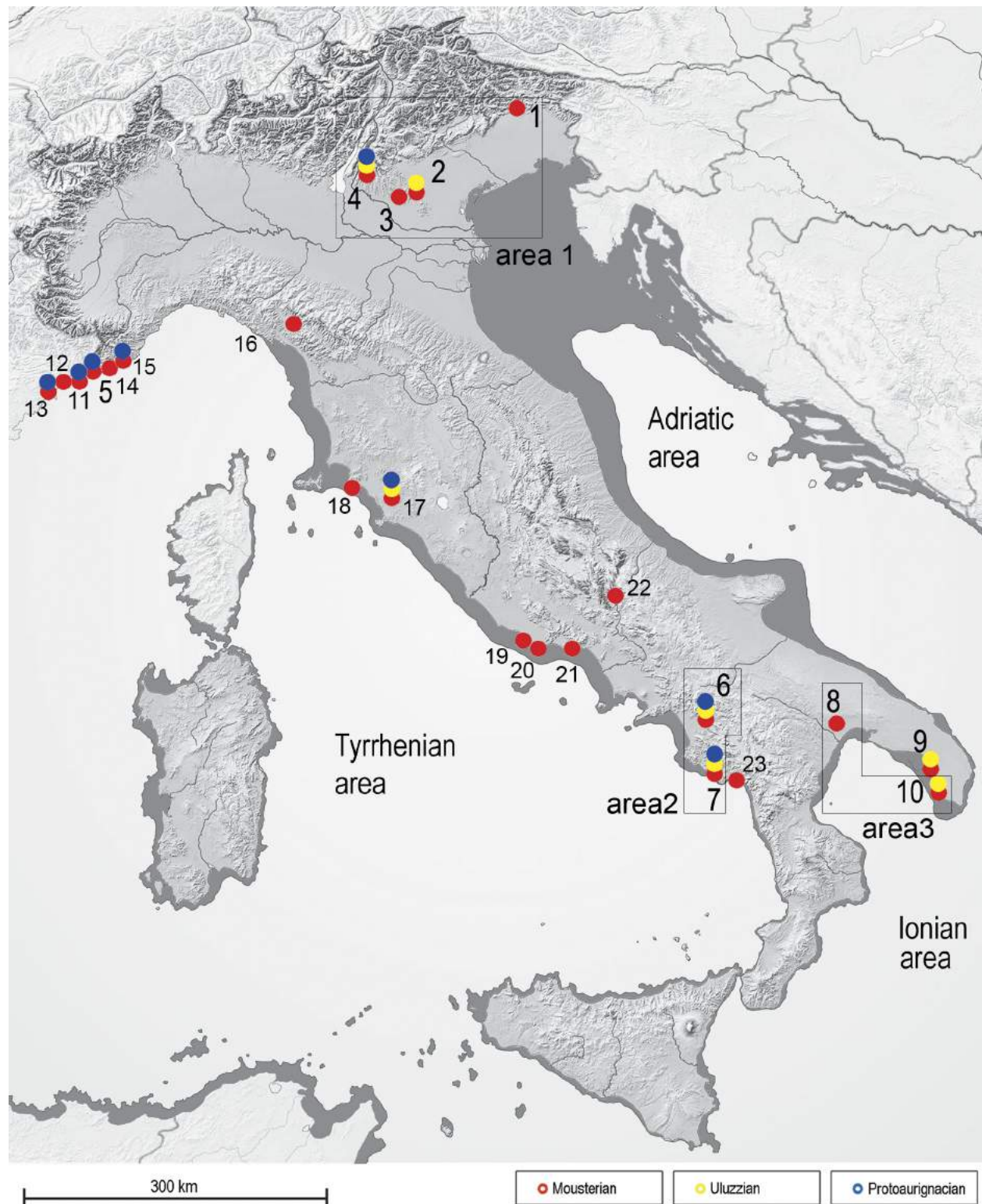




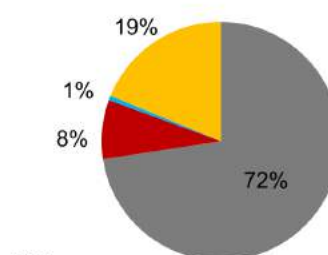
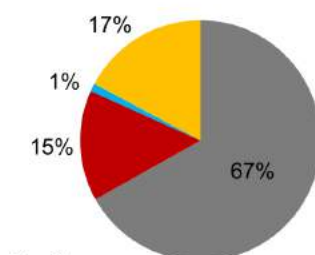
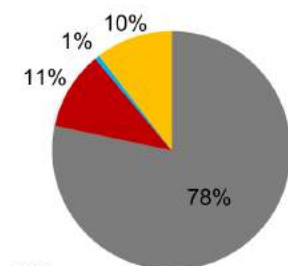




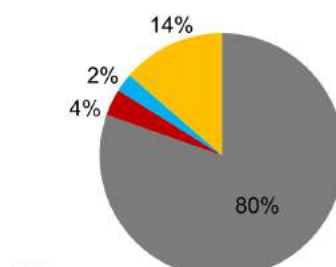
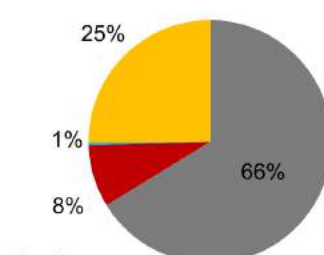
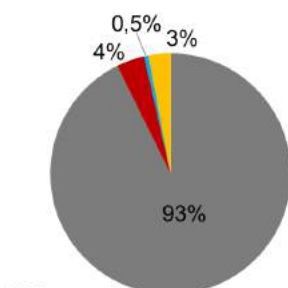




## NORTHERN ITALY



## SOUTHERN ITALY



■ UNGULATA ■ CARNIVORA ■ RODENTIA - LAGOMORPHA ■ AVES

